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WILLIAM GILSON FARLOW[1]

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Since the death of Asa Gray, in 1887, no American botanist has been accorded quite the esteem in which Professor Farlow was held. As with Bornet, this was due even more to a large influential acquaintance and a recognized conservative well-informed sanity in judgment, than to volume or importance of the publications of his later life. Indeed, for some years past he has been rather hesitant about putting into print things that he knew better than others—possibly through the realization of age, that nothing is really finished even when an expert gets to the end of what he can do with it; that sometime or other somebody else can go as far; and that in any event somebody else will have to start again at the beginning, sometime or other.

Merely to possess a large acquaintanceship does not mean necessarily that a man will be liked or admired or respected. Professor Farlow's personality was such that with few and unimportant exceptions the many who had the privilege of knowing him liked and admired and respected him to an unusual degree. His character and talent and learning were such as to command affection, admiration, and respect. If either attribute was ever withheld by a colleague or acquaintance it was because of an utter failure to understand his nature, which did not court praise or deference and sometimes in an effort to escape one or the other prompted a seeming cynicism or levity which was as unreal as it was ready and brilliant.

Dr. Farlow was characterized not only by an artistic temperament but by unusual quickness of perception and response. Those who knew him best were likely to hesitate before engaging him in even the most friendly of bantering encounters: but his tongue was not sharp for those of whom he disapproved, and when he wanted to bring a thing into question he had the art of doing it by some most inoffensive but nevertheless unmistakable anecdote or figure of speech.

Men who enlist the interest of others differ greatly in the way in which they communicate their own enthusiasm. Gray bubbled over with it as he worked and talked. Farlow was much less effusive, but those who were

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privileged to know him and study under his supervision saw his manifest interest in their work and imbibed some of his unobtrusive enthusiasm over his own work. It is unlikely that any student who came near enough to him in space or age or mentality really to know him, remembers him more vividly in any respect than as a kind friend—observant, thoughtful, and helpful, but with a tact that prevented any impression that he saw the need of the help that he gave.

In the history of American botany, Professor Farlow figures as the personality through whom thallophytes passed into the field of college botany. Classic work had been done on them by men not filling college chairs, and voluminous work of lasting value continues to be done by such men: but it was his privilege to teach as well as to investigate in this field. He considered himself a botanist rather than a phycologist or a mycologist, and he never called himself a phytopathologist.

Many of his published papers deal with the algae, and his opinion on our seaweeds was taken everywhere and always as authoritative; but he did not train many men in their study. When his own opportunity to work under a master came, it was the fungi that he elected, and De Bary to whom he went; and his greatest service as a teacher and an investigator was rendered in this special field of botany, out of which the half-segregated practical applications of plant pathology evolved during his lifetime.

Though never very robust, and subject to frequent distressing if not serious ailments, Dr. Farlow was an indefatigable worker and an insatiable reader—never satisfied with what somebody said that somebody else had said. During the later years of his life he was freed from the burden of teaching, but compelled to shoulder a business responsibility involving the administration of large financial interests. He neither had nor apparently wished the relaxation commonly considered the due of a septuagenarian. Like the friend and mentor of his youth, Asa Gray, he died in the harness; and the great herbarium and library that he has left to Harvard University with a liberal endowment will keep in memory the debt of his Alma Mater and of the botanical world to him, our foremost authority on the thallophytes, as effectively as the greatest student of American flowering plants is commemorated in the Gray Herbarium of the same institution.

The traits which marked Professor Farlow's mature and professional life were forecast in his descent and development. He was born and educated in Boston. His parents were of New England stock, and his father in addition to being a successful business man was active in public service and a supporter of horticultural and musical organizations. As a student he was as brilliantly diverting as his intimates found him to be in later life, with a penchant for natural history. He graduated from Harvard College in 1866 and from the Harvard Medical School in 1870, and for the next two years assisted Professor Gray in the botanical department of the college. The next two years were spent in Europe, partly in travel and

y as a graduate student at Strasbourg. For several years after his n home he taught in the Bussey Institution of Harvard University as ant professor of botany; but from 1879 until his retirement from e service in 1896 he taught in Cambridge, with the title of professor of ogamic botany, which he held up to the time of his death, when he had ne the senior member of the faculty.

Publications

The following list of Dr. Farlow's publications has been prepared from memoranda furnished by Mr. A. P. D. Piguet and is as nearly complete as it has been possible to make it, except that none of his numerous reviews of books and articles have been included.

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1872. Marine algae. Proc. Boston Soc. Nat. Hist. **14**: 64.

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1874. Notes from the journal of a botanist in Europe I. Amer. Nat. **8**: 1. II. Amer. Nat. **8**: 112. III. Amer. Nat. **8**: 295.

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An asexual growth from the prothallus of *Pteris serrulata*. Proc. Amer. Acad. Arts and Sci. **9**: 68.

1875. List of the marine algae of the United States, with notes of new and imperfectly known species. Proc. Amer. Acad. **10**: 351.

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1876. Gustave Thuret. Journ. Bot. **14**: 4.

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On the American grape vine mildew. Bull. Bussey Inst. **1**: 415.

Synopsis of the Peronosporeae of the United States. Bull. Bussey Inst. **1**: 426.

List of fungi found in the vicinity of Boston. Bull. Bussey Inst. **1**: 430.

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University instruction in botany. Amer. Nat. **10**: 287.

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The sea weeds of Salt Lake. Preliminary report. Amer. Nat. 13: 701.

1880. On the nature of the peculiar reddening of salted codfish during the summer season. Rept. U. S. Fish Comm. 1878: 969.

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Montia sibirica in Massachusetts. Rhodora **18**: 240.

Jean Baptiste Edouard Bornet. Proc. Amer. Acad. **51**: 852.

THE DEVELOPMENT OF THE THALLUS OF SPHAEROCARPOS DONNELLII AUST.

H. W. Rickett

The Germination of the Spore

Previous descriptions of the germination of the spore of Sphaerocarpos represent two conflicting views. One of these is held by Leitgeb and Goebel, the opposing one by Campbell. These are the only authors who have described spore germination in Sphaerocarpos. Leitgeb (9), the first to study this subject, identifies the method of spore germination with that typical for the Ricciaceae and Marchantiaceae. There is, according to him, a germ tube formed, consisting at first of a single cell, and later of several tiers of cells arranged in groups of four. The terminal quadrant of this structure forms the germinal disc, and one of its cells becomes the apical cell of the thallus. The latter grows out in a plane at right angles to the long axis of the germ tube. The apical cell is at first two-sided, cutting off two sets of lateral segments; it is later replaced by a four-sided apical cell, forming dorsal and ventral segments in addition to the lateral ones, and thus causing the thickening of the thallus. The first rhizoid is formed very early, but he states that its connection with the sporeling was to him obscure, though obviously arising from a previous division of the original cell.

Campbell (3), studying spore germination in Riccia, was unable to confirm this account; according to him growth is continuous in one direction throughout the history of the sporeling, and there is no formation of a germinal disc or plate on the end of, and at right angles to, the germ tube. According to his description, the germ tube, consisting of several tiers of cells, is formed as described by Leitgeb, and from one of the terminal cells a two-sided apical cell, later replaced by a four-sided cell, is formed; but growth resulting from the segmentation of this apical cell takes place in the same direction as does that of the germ tube. He agrees with Leitgeb in classifying Sphaerocarpos with the typical Ricciaceae and Marchantiaceae so far as the method of spore germination is concerned, but differs from him in his description of the method by which this takes place. In his account of the process in Sphaerocarpos (2), he describes in detail the way in which the two-sided apical cell is replaced by a four-sided cell. The two-sided cell is divided by a basal (posterior) wall in a vertical transverse direction, and then begins to cut off three sets of segments instead of two, two lateral and one basal. Later, two sets of basal segments are formed, the one basal wall being replaced by two inclined to one another. Thus finally four sets of segments are formed, two lateral, one dorsal-posterior, and one

ve -posterior. He gives no details as to his method of studying this tr rmation. Campbell also states that the first rhizoid grows from the ba ell of the germ tube near the spore wall. It is not usually formed until th ung plant is multicellular, and it is not separated from the germ tube by all. Later rhizoids arise from the older cells of the young thallus.

ebel's description (7) in general confirms that of Leitgeb. According to m, however, it is impossible to say that the thallus develops from a sin cell of the terminal quadrant of the germ tube, which cell functions as apical cell from the beginning. On the contrary, all the cells of this germinal disc take part in the growth of the thallus, an apical cell is discernible only at a later stage, and one cannot determine from which cell of the germinal disc it was developed. He tends to bring together the two opposing views of Leitgeb and Campbell by calling attention to the fact that the fo mation of the germinal disc is not the development of a new structure from a sort of protonema, but is rather a simple flattening out of the young thallus presumably as a response to external conditions of air and light. The chief evidence in favor of this idea is found in a comparison with the method of growth in regeneration, which may resemble either description of the method of spore germination. He contrasts this type of development, which he calls "homoblastic," with that of the "heteroblastic" sort, in which the body of the plant arises secondarily from some sort of protonema.

A difference in species may perhaps account for the difference in descriptions. Campbell, according to Miss Haynes (8), was working with either (or both) *S. texanus* or *S. cristatus*. The European authors probably studied *S. Michelii* and *S. texanus*. It is also, of course, not inconceivable that differences in climate and in general habit might influence the course of development.

The description which follows is based on a study of sporelings of *S. Donnellii* grown from spores sown broadcast in a mixture of clay loam and sand and kept in a Wardian case in the greenhouse. When the young plants became visible under a hand lens as minute, bright green growths on the surface of the soil, they were picked up with a needle under a binocular microscope, the soil was washed off in water, and the plants were mounted in glycerin. A solution of chrom-acetic acid (chromic acid, 0.3 g.; glacial acetic acid, 0.7 cc.; distilled water, 99 cc.) proved most satisfactory for fixing. Various attempts were made to stain the sporelings, but without much success. They took the stain with difficulty, and it did not prove permanent. However, since in most cases the cells were slightly plasmolyzed, the cell walls stood out fairly sharply although they did not always maintain exactly the original form of the cells.

Different attempts were made to germinate spores in culture solution, using that recommended by Marchal and Marchal (10), but it was impossible to keep the cultures free from fungi brought in on the spores or on

small shreds of tissue. In some cases germination occurred, after about twice the normal period, and resulted in the production of some abnormal plants. I was unable to grow any of these plants to maturity, on account of the fungous growth which soon covered and choked them.

The spores sown in soil germinated usually about a month after sowing, in the case of those sown early in the spring. Some sown in early summer required three or four months to germinate. The first sign of germination is the appearance of a slender germ tube which pushes out through an irregular ruptured spot in the heavy spore wall. The spores from a greenhouse culture are at this time still united in tetrads, which is contrary to the usual description for *S. Donnellii* under natural conditions (8). The spores of a tetrad do not usually all germinate at the same time, and it is rare to find a tetrad with all four spores producing young plants. The germ tube is filled with dense cytoplasm, and contains from the first an abundance of chlorophyll, and there are often present in the early stages globular bodies having the appearance of oil droplets. As the tube grows in length, the dense contents become gathered at the distal end, leaving the basal end almost clear and quite colorless, and the first wall usually cuts off a terminal cell which contains all, or nearly all, of the dense cell contents. The length to which the germ tube may grow before the first cell division occurs varies considerably. This is evident from a comparison of figures 1 and 2, Plate IX. In cases in which I have made measurements, the length of the undivided germ tube varies from 0.3 to 1.6 mm. The majority of the germ tubes reach a length of about 0.5 mm. by the time of the first cell division. In the cases of the abnormal sporelings mentioned above which resulted from spores germinated in nutrient solution, the most remarkable feature was the great length to which the germ tube attained. It seemed to be able to grow indefinitely until the distal end reached the surface of the solution, at which time cell division usually occurred (fig. 35, Pl. X). Some that I have measured reached a length of 7 or 8 cm., and consisted of a single long hair-like cell with a small mass of dense green material in the extreme distal end, and only to be distinguished by this latter characteristic from the rhizoids produced at the same time.

The first wall is transverse, and divides the germ tube into a large clear basal cell, from which only the first rhizoid develops and which undergoes no further division, and a small, densely-filled terminal cell from which the rest of the young thallus develops (fig. 2). The basal cell persists for some time, so that the young plant remains attached to the spore wall until well along in its development—until about the time when the secondary disc begins to be composed of two cell layers.

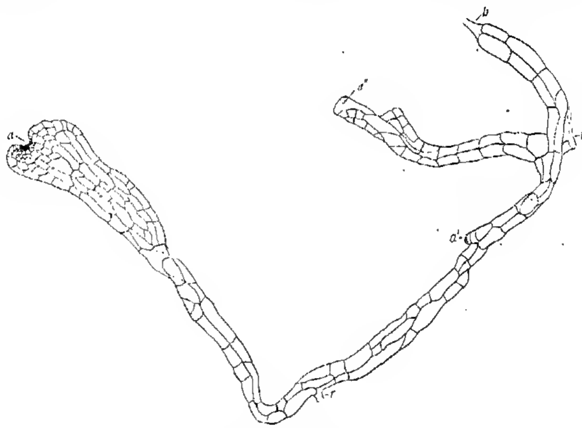
The second cell division occurs in a plane parallel to the first, cutting the terminal cell into two (fig. 3). About this time the first rhizoid usually appears, pushing out from the extreme base of the germ tube, and growing rapidly in the opposite direction. It is a simple slender structure, almost devoid of granular contents except at the extreme tip.

The next division is variable, and indeed the whole subsequent history, up to the time when the young thallus has been fully formed, is very inconstant. Figures 4 to 9 indicate some of the methods by which the development occurs. The end cell resulting from the second transverse division may divide longitudinally (fig. 4), or other transverse walls may first be put in, and any of the resulting cells may divide longitudinally (figs. 5, 7). The result is usually the same in all cases—namely, the formation of a small plate of cells (commonly six or eight) of about equal size arranged in pairs (figs. 6, 8). Occasionally, however, some of the longitudinal divisions may fail to occur, the result being a single cell at some point in the double row of cells in place of a pair of cells (figs. 7, 9, 11). The next divisions are also longitudinal, but at right angles to the preceding, the result being a series of several groups of four cells each, with, however, many departures from absolute regularity. Very frequently the groups consist of three cells instead of four. The arrangement of cells here is difficult to determine under the microscope, as dividing walls are often either in the plane of the slide or superimposed vertically one upon the other. Figures 13, 20, 21, and 23 represent the arrangement of the cells at this time. These figures are of older stages in the development of the thallus, but all the cells except those of the terminal group have remained undivided.

The cells of the end group now begin to divide, mostly by longitudinal walls, so that a plate of small cells is formed at the end of the germ tube (figs. 10-16). These divisions are apparently more rapid than those preceding, since the cells do not attain so large a size before redividing. The divisions seem to be quite irregular, and I failed to find any cell in these stages which could be recognized as an apical cell. In figures 10 and 12 there is shown a cell (*a*) cut off by a diagonal wall suggestive of the apical cell described for many liverworts; this appearance, however, is not the usual one. The typical appearance of the young thalli at this stage is best shown in figure 13. The groups of cells below the terminal plate undergo no further divisions, though rhizoids are often produced from them; the rest of the thallus develops entirely from the germinal disc. This disc is very conspicuous, though in certain views, when mounted and observed under the microscope, it is sometimes flattened out so as to suggest a flat plate growing in the same direction as that of the original tube (fig. 26), instead of being placed at right angles on the end of the latter. I have seen cases in which the direction of growth of the plate seemed really to be a continuation of that of the germ tube, but in all but one of these (fig. 24, Pl. XII) the sporeling had become separated from the spore wall, and hence could not be distinguished with certainty from the not infrequent cases of regeneration from small shreds of tissue in the soil. Regenerative shoots take on many different appearances, and often seem to grow for a time by means of a single two-sided apical cell, which is regularly wedge-shaped. The only resemblance to this condition that I have found in sporelings is in

those grown in nutrient solution; in these instances the terminal cell seemed to function as an apical cell, forming a narrow ribbon composed of pairs of cells (figs. 35, 36, Pl. X), the whole gradually broadening out into a flat plate. In the latter stage, however, the appearance of an apical cell was lost, and lateral growing points often appeared, from each of which presumably, under favorable conditions, a thallus would have developed (fig. 37, Pl. XII; text fig. 1).

After the terminal disc has been formed, its further growth usually becomes markedly one-sided. This results from the development of a group of rapidly dividing initial cells at one side of the disc. This tendency is illustrated in figures 15, 17, etc., Plate IX. Division in this group of cells takes place in several planes all at right angles to the original divisions of the germ tube, so that a flat plate, one cell thick, grows out at right angles



TEXT FIG. 1. An abnormal thallus which resulted from a spore germinated in nutrient solution: *a*, *a'*, *a''*, apical regions; *b*, basal cell; *r*, rhizoids. The cell walls at *a'* could not be seen on account of the density of the cell contents. Drawn from living material, × about 50. Compare figures 35 and 36, Plate X, and figure 37, Plate XII.

to the latter. At first the plate is cup-shaped, owing presumably to the more rapid growth of the edges; later, however, it spreads out into a flat blade. This process is illustrated in figures 17 26, Plates IX and XII. It is noteworthy that one of Campbell's figures (3) of a sporeling of Riccia bears a strong resemblance to some of these figures, such as figure 23. In most cases, growth occurs by the division of a few cells at one point on the margin of the plate. Sometimes two such groups of initials may be formed, resulting in a marginal growth of the thallus at two points (*a*, *a'*, figs. 27, Pl. XII, and 28, Pl. X). In the particular case shown in figure 27 there is

a c[...] t the apex of each lobe that has very much the appearance of an apic[...]ell; but this is the exception rather than the rule. The typical group of [...]l cells is shown in figures 26 and 30–34 (Pls. IX, X). It consists of a [...]rginal row of small cells of dense contents, rather longer than wide, all [...]stantially alike as to size and shape. As these cells continue to divi[...] not enlarging to any extent, the segments cut off from them on the [...]tside outstrip them in growth and form two lobes, one on each side of t[...] apical region. This results in the formation of an apical notch, which may be median (figs. 26, 32, 33) or lateral (fig. 34). The lateral position of the apical notch is a common appearance; it is noted in the subsequent history of the plant in the formation of a small and a large lobe on opposite sides of the growing point, and frequently in the formation of short branches when the growing point forks.

After the young thallus has reached this stage in its development, it becomes more than one cell thick in the central portion. Just how this transformation is effected I have been unable to determine. Mounts *in toto* no longer prove satisfactory, owing to the density of the cell contents in the apical region; and the plants are still too small to be handled readily by ordinary methods of fixing and sectioning.

Apical Growth and the Formation of the Thallus Lobes

Both Campbell (2) and Leitgeb (9) describe the growth of the thallus as being due to a single apical cell which cuts off right and left lateral segments and dorsal and ventral segments. Campbell says that the lateral segments so resemble the apical cell in horizontal view that it is difficult to say with certainty that there is but one apical cell. Leitgeb describes the apical cell as lying at the deepest point of the notch in the forward margin of the thallus, and states that this notch is often so narrow that there is space only for a single small cell. He goes on to say, however, that sometimes the notch is broader, and more rarely it is quite wide, which appearance, he thinks, is a sign that forking is about to occur. The situation throughout, according to Leitgeb, is practically the same as that found in typical Ricciaceae and Marchantiaceae.

It is a difficult matter, in mature plants, to obtain sections passing through the growing point exactly in a longitudinal vertical direction, owing to the small size of the plant, and to the presence of a mass of involucres and lobes about the growing point. In many hundreds of slides, I have obtained two satisfactory series of sections of the growing point cut in this plane (figs. 38–54, Pls. X, XI), and some rather less satisfactory series cut in horizontal and in transverse vertical planes (figs. 55–67).

The plants which I studied were grown in a Wardian case in the greenhouse, and the shady conditions, the abundance of moisture, and the absence of any seasonal limitations of the growing period, were responsible for a more luxuriant growth of the thallus, with a corresponding increase

in the size and number of the lobes, than is the case under natural conditions. The thallus, instead of being a simple small plate, the edges of which are cut into more or less crowded and overlapping lobes, as is the case in nature, took on the form of a central thick, distinct axis bearing leaf-like lobes irregularly on either side, and attaining a considerable size. The involucres also grew longer and were more cylindrical in form, the mouths often flaring out and becoming undulate. These peculiarities are even more noticeable if the plants are grown in petri dishes on filter paper moistened with a nutrient solution (fig. 70, Pl. XII). Campbell (2), working, according to Miss Haynes (8), on a mixture of *S. texanus* and *S. cristatus*, described similar forms occurring in nature under exceptional conditions of moisture and shade, but in these cases the production of sex organs was partly arrested, whereas in the plants I studied rather the reverse was true. The Douins (4, 6), studying *S. Michelii and S. texanus*, also mention the growth of abnormal plants under cultural conditions. According to the description of C. Douin (4), the plants usually possess in nature three large lobes with a mall "middle lobe" in each of the two apical notches. The figures of Allen (1), however, made from living plants grown under natural conditions, show a less schematic and more luxuriant growth.

Leitgeb (9) says that the lateral segments of the apical cell continue for a time to cut off dorsal and ventral segments in the same manner as the apical cell itself, but sooner or later a lobe cell is formed, which grows out by vertical divisions into one of the lobes. This is the same condition as is shown by longitudinal vertical sections through the apical region (figs. 38–54). In such a case it is extremely difficult to determine whether there is a group of apical cells present, or a single apical cell, which has formed new apical cells to either side in preparation for a forking of the growing region. My figures show several small cells, having the shape usually described for the four-sided type of apical cell, grouped together in the apical region (*a*, figs. 38–54); and, in the case of one of the apical regions illustrated, several such groups are present, each two consecutive groups separated by a young lobe (*l*, figs. 38–48). The presence of several groups of initial cells indicates presumably that the original group had divided several times in close succession, the intervals between the groups being occupied by lobe cells. This is usually the case under cultural conditions, and dichotomy is correspondingly rapid. An examination of the plants under a hand lens confirms this interpretation of the figures. The apical region is often very wide, and there are usually from one to four small lobes in it. The fact that each group of initial cells consists of cells all alike and all having the appearance of four-sided apical cells, seems rather to favor the idea that growth is not due to a single apical cell but to a group of initials. It may be, of course, that the condition depends upon the environment, and that in nature a single distinct apical cell exists, while in culture this single cell is multiplied without a corresponding forking of the growing region necessarily resulting.

The existence of a group of initial cells is similar to the condition in Marchantia as usually described. Mottier (11), however, inclines to the view that in Marchantia also only one apical cell is present.

In longitudinal vertical section these initial cells (*a*, figs. 38–54) are regularly wedge-shaped, cutting off narrow segments mostly, but not always, in alternate succession. Archegonial initials may be seen, as described by Leitgeb (9), Douin (5), and others, only one or two cells distant from the initial cell or cells, each apparently formed from an entire dorsal segment of the latter (*ar*, figs. 38–54). From the ventral segments mucilage hairs grow out, each consisting of a row of cells, the terminal cell being large, spherical, filled with dense contents, and provided with a large nucleus (*s*, figs. 38–54). In the preparations these mucilage hairs become more or less shrunken and torn.

Sections cut through the growing region in a horizontal and in a vertical transverse plane are less satisfactory than those just described, owing to the even greater difficulty of orienting the plants in the paraffin for this purpose. Figures 55–61, Plate XI, illustrate a series of horizontal sections, starting at the ventral side. The small cells marked *a* in figures 59 and 60 probably represent the apical group. They are noticeably more dense in content than any other cells in the sections, except those of the mucilage hairs. They are obviously dividing with considerably rapidity; and the varying length of the same cells in succeeding sections (*x*, figs. 59, 60) makes it probable that they are bounded posteriorly by an inclined wall, and therefore correspond to the initial cells shown in the vertical sections. The sections suffer from the fact that they are cut at a slight angle from the horizontal.

Figures 62–67, Plates X and XI, illustrate similar groups of cells as seen in vertical transverse section. The first series (figs. 62–64) is taken from a very young thallus, consisting of a simple plate one cell thick in all parts save in the center, where the cells are smaller, denser, and obviously embryonic. At the beginning of the series (fig. 62) there are two plates of cells, one cell thick, separated by an empty space—the apical notch—instead of by the group of initials. At one side in the drawings (*x*, figs. 63, 64) there are several large hyaline cells which disturb the otherwise symmetrical arrangement. This is probably due to a fold in the thin thallus-blade. Figures 65–67, Plate X, illustrate a similar series from a mature plant. Here also a group of similar embryonic cells (*a*) is present; but in this case they are cut slightly on a bias, so that at one side they seem to merge into a mature lobe (*l*), while at the other side there is no corresponding structure. It is unfortunate that none of the sections except those cut in the longitudinal vertical plane showed the young lobes so evident in the latter; unless the cells marked *y*, figures 57–60 (Pl. XI), may be interpreted as such.

A second method was used in order to determine the origin of the lateral lobes of the thallus. Single plants were isolated and grown in

separate pots, and sketched each day under a binocular microscope. Young plants with only two or three lobes were selected in most cases, and watched in this way until they had attained the size of normal mature plants. The lobes differ sufficiently in shape and size so that one can feel certain that one is following the growth of each individual lobe from its beginning until maturity. The plants were kept in the Wardian case and showed the peculiarities of growth already described.

This study shows that the lobes of the thallus are formed at the tip and are pushed back into a lateral position, as they increase in size, by the elongation of the median portion of the thallus, or midrib. It is also seen that they are not "middle lobes" in the ordinary sense, that is, lobes produced simply by the outgrowth of the thallus between two divisions of the originally single growing region; for very commonly two lobes are formed at the same time, without any consequent branching of the thallus. If all the notches between the lobes represent divisions of the apical region, it must be that some of these branch regions are arrested in further development, and that their cells merely mature without dividing further. When one lobe is formed singly, it often resembles the ordinary "middle lobe" of such a form as *Ricciocarpus natans*, and the growth of the thallus continues on either side of the lobe. This, however, is not necessarily the case, since in many cases only one of the regions to either side of the lobe produces new growth, the middle lobe being pushed aside and coming to lie on one side of the central axis, without a corresponding lobe on the other side. This is of common occurrence, and is often responsible for the curving growth of the thallus as a whole.

In the light of the foregoing studies, therefore, it is reasonable to suppose that a lobe is formed by the occurrence of vertical divisions in a lateral segment of an initial cell, and this, as both the sections and the study of living plants show, may, at least in greenhouse cultures, occur anywhere in the apical region, irrespective of divisions of the latter.

In nature, the growth of the thallus, to judge from the accounts of previous authors, is apparently much like that of Riccia. According to Douin's (5) description of Sphaerocarpos, there are usually two notches, separated by a large middle lobe, present in a mature plant. In the notches are usually two other small lobes, with a growing point on either side—thus four growing points in all. At this point, he says, growth usually stops, though it is not uncommon to find plants having five large lobes with small ones in each notch. The growth, of course, is limited by the end of the growing season. The only difference between this history and that of Riccia, according to the same author, is the fact that in Sphaerocarpos the middle lobe remains undivided, whereas in Riccia it becomes cleft as the midrib elongates. Hence in the latter case the growth of the midrib is more rapid than the intercalary growth at the base of the lobes, while in the former case the reverse is true. In nature, evidently, the lateral seg

rows of initial cells of the apical region merge together in their development to form the broad marginal wing of the thallus; while in culture the more rapid growth of the central portion of the thallus causes the separation of the tissue developed from each cell into separate lobes.

In the plants grown in culture, the involucres are often broadly open at the tip and show various irregularities in form. Dorsal lobes were observed in several cases, and there are gradations between these dorsal lobes and the normal involucres. The Douins (6) also mention these peculiarities. This suggests the idea that the formation of lobes and that of involucres may be intimately connected, and that the form of the entire plant may depend rather strictly upon the environment. One might go even farther and suggest that there is an evolutionary relationship between some of the higher lobed or leafy liverworts and the various forms assumed by the more primitive types. There is at least a close resemblance. In *Pellia epiphylla*, according to Douin (4), of two middle lobes produced by the forking of the growing point, one is arrested in growth, while the other continues its development, and then a new lobe appears in the notch between them, thrusting to one side the lobe which has ceased its growth. The lateral lobes of many liverworts may be formed in this way.

Plants grown under water by regeneration from involucres and from lobes cut off from the plant show the same abnormalities as those above described carried to an extreme, except that there is little or no branching and that sex organs are not abundant. The plant consists of a long almost cylindrical axis, bearing a few scattered and small leaf-like lobes.

The following is a detailed account of two of the plants studied as indicated above. They are typical of the history of all the other plants studied, so that it is needless to multiply examples.

Plant no. 1. Lobes *a*, *b*, *c*, *e*, and *f* (fig. 68 *A*, Pl. XII) have already reached maturity, and do not change their position in the subsequent history of the plant; they may increase slightly in size. Lobe *d* is an example of a "middle lobe," growing regions developing on either side of it. However, in the notch to the left of it, a single lobe forms (*g*, fig. 68 *B*), on only one side of which—between lobes *g* and *d*—is there any further growth. In the notch between these two lobes growth proceeds in the usual way. On the other side of *d*, at first only one lobe—*h*—is visible (fig. 68 *B*), but another—*i*—soon makes its appearance (fig. 68 *C*), and finally comes to equal *h* in size. This sort of thing is of common occurrence, and indeed the formation of these little lobes exhibits the greatest variability as to size, shape, number, and time of appearance. The further history of this plant illustrates how the lobes are pushed into a lateral position, while new lobes arise at the apical region. In the last sketch (fig. 68 *D*), lobes *h* and *i* are approaching their mature size, and two small lobes have made their appearance simultaneously between them. On the other side of lobe *d*, meanwhile, two lobes (*k* and *j*) have developed at the same time (fig. 68 *C*), and finally

(fig. 68 *D*) are considerably spread apart and a single lobe is to be seen between them.

Plant no. 4. The two forward lobes, *a* and *b* (fig. 69 *A*), are spread apart until there is a wide notch between them and they occupy a lateral position (fig. 69 *B*). This notch is filled by a round mass of cells. Two new lobes, *c* and *d* (fig. 69 *C*), are formed simultaneously in this notch, at first being in a transverse and nearly vertical position. (In the drawing, these two lobes appear to be of dorsal origin. This is not actually the case, the illusion being due merely to the position in which the plant was seen when sketched.) These two lobes are then subjected to the same process of spreading, and a few days after (fig. 69 *D*) a new lobe, *e*, has appeared between them. Three days after this, this lobe has reached a considerable size, and there is a new small lobe on either side of it—lobes *f* and *g* (fig. 69 *E*). This occurrence of three lobes, not widely different in size, is also very common. In the last stage sketched (fig. 69 *F*), a single lobe—*h*—again appears on one side of this "middle lobe," and on the other side two small lobes, *i* and *j*, are formed at the same time. In the subsequent history of this plant, the formation of lobes went on in the same way, small lobes succeeding each other rapidly in a very various and complicated manner, with no apparent relation to the occurrence of branching except sometimes in cases where only a single lobe was formed at one time (*e.g.*, lobe *e*, fig. 69 *F*).

Branching always occurs by the division of the apical region. In nature it is limited by the short growing season of the plant, and the number of growing points found in plants living under natural conditions, as described by Douin, has been referred to above. In culture, however, the plants may live indefinitely, and profusion of branching is in keeping with the luxuriant habit of the plant as a whole under greenhouse conditions; and owing to the rapid elongation of the central axes of the branches, the latter are more easily distinguished from each other. By the gradual dying of the posterior part of the thallus, branching, under the conditions referred to, is an effective means of vegetative multiplication.

Summary

1. The spore of *Sphaerocarpos Donnellii* germinates by means of a slender filament of cells, the germ tube, on the end of which, and at right angles to it, is formed a germinal disc. The latter structure develops into the thallus of the mature plant.

2. The history of the formation of the germ tube is very variable.

3. The growth of the germinal disc does not seem to be due to the activity of a single apical cell, except in special cases. It is formed by divisions of all the terminal cells of the germ tube, and continues its growth through the activity of a group of cells on the margin which remain embryonic in character.

4. The apical growth of the mature thallus is due to a group of cells occupying the apical notch. These cells have the appearance of four-sided apical cells. The lateral segments which they cut off either resemble the mother cell, or go to the formation of the thallus lobes. The dorsal and ventral segments add to the thickness of the thallus in the median portion.

5. The marginal lobes of the thallus are formed by the division of lateral segments of the apical cells. Under natural conditions, successive lateral segments merge together in their development to produce a more or less continuous marginal wing. Under cultural conditions, the more rapid elongation of the median portion of the thallus causes the separation of the structures derived from individual lateral segments into distinct leaf-like lobes, attached laterally along a central midrib.

6. Branching of the thallus is due to a division of the apical group of cells into two such groups, a lobe occupying the region between. The formation of lobes is not necessarily related to branching.

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EXPLANATION OF PLATES IX–XII

All drawings, except figures 68, 69, and 70, were made with the aid of a camera lucida. In these cases the drawings were freehand sketches of plants as seen under a binocular microscope. Figures 25, 35, 36, 37, 68, 69, and 70 were made from living plants. Magnifications given are approximate.

FIG. 1. Undivided germ tube. × 150.

FIG. 2. First division of the germ tube: *sp*, spore wall. × 150.

FIG. 3. Second division of the germ tube. × 150.

FIG. 4. Third division of the germ tube: *sp*, spore wall; *r*, rhizoid. × 150.

Figures 1–4 are shaded to indicate the distribution of the dense cell contents.

FIGS. 5–9. Further divisions of the germ tube, prior to the formation of the germinal disc: *sp*, spore wall; *b*, basal cell. × 150.

FIG. 10. Beginning of the formation of the germinal disc: *a*, possible apical cell. × 350.

FIG. 11. Further divisions in the formation of the germinal disc: *b*, basal cell. × 150.

FIG. 12. The same: *a*, possible apical cell; *b*, basal cell. × 350.

FIG. 13. Two sporelings at the time of formation of the germinal disc: *sp t*, spore tetrad; *r*, rhizoid; *g*, germinal disc. × 50.

FIG. 14. Formation of the germinal disc (compare fig. 13, *g*). × 350.

FIGS. 15–23. The young germinal disc. × 150.

FIG. 24. Young thallus continuing its growth in one plane, without formation of a germinal disc: *a*, possible apical cell; *sp*, spore wall. × 75.

FIG. 25. Germinal disc in a more advanced stage: *a*, apical region (the cell contents too dense to permit of the cell walls being distinguished); *b*, basal cell; *c*, place of attachment of the germinal disc to the germ tube. × 75.

FIG. 26. The initial cells at the apex of a young sporeling. × 150.

FIG. 27. Young thallus growing out in two directions, and possessing two apical regions: *a*, *a'*, apical regions; *c*, place of attachment of germinal disc to germ tube; *b*, basal cell. × 75.

FIG. 28. The apical regions of the plant shown in figure 27: *a*, *a'*, possible apical cells. × 150.

FIG. 29. The point of attachment of germinal disc to germ tube. × 150.

FIG. 30. Initial cells of a young sporeling. × 150.

FIG. 31. The same. × 350.

FIGS. 32, 33. The same in slightly older sporelings, showing the formation of the apical notch. × 150.

FIG. 34. The formation of the apical notch in a lateral position. × 150.

FIG. 35. Abnormal sporeling from a spore germinated in nutrient solution. × 25.

FIG. 36. Detail of figure 35. × 150.

FIG. 37. Another abnormal thallus produced in the same way: *a*, apical region; *r*, rhizoid. × 75.

FIGS. 38–48. Series of longitudinal vertical sections through the apical region of a mature plant: *a*, apical cells; *ar*, archegonia; *i*, involucres; *l*, lobes of the thallus; *s*, mucilage hairs. × 350.

FIGS. 49–54. Another series of sections through the apical region of a mature plant, cut in the same direction as the preceding: *a*, apical cells; *ar*, archegonia; *ar in*, archegonial initials; *i*, involucres; *l*, lobes of the thallus; *s*, mucilage hairs. × 350.

FIGS. 55–61. Series of horizontal sections through the apical region of a mature plant. Two sections omitted between figures 60 and 61. The first figure of the series is on the ventral surface of the apical region, the last one on the dorsal surface: *a*, apical cells; *ar*, archegonium; *ar in*, archegonial initial; *l*, lobe of the thallus; *s*, mucilage hairs; *x*, see text; *y*, possible lobe. × 400.

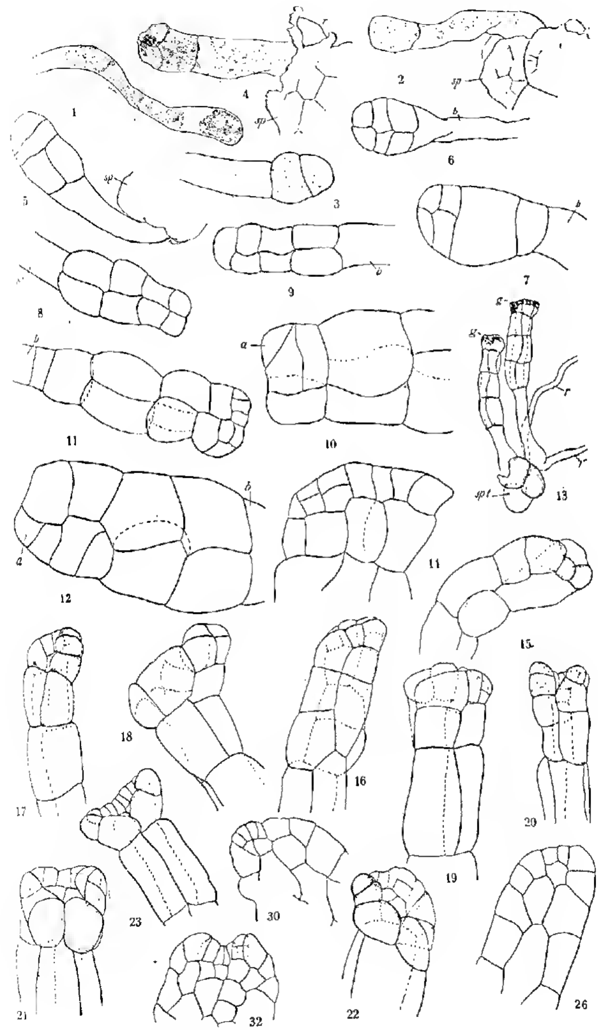
FIGS. 62–64. Series of vertical transverse sections through the apical region of a young plant: *a*, apical cells; *s*, mucilage hair; *X*, see text. × 400.

FIGS. 65–67. Series of sections through the apical region of a mature plant cut in the same way as the preceding series, but in a plane not quite perpendicular to the axis of growth: *a*, apical cells; *ar*, archegonia; *i*, involucres; *l*, lobe of the thallus; *s*, mucilage hairs. × 350.

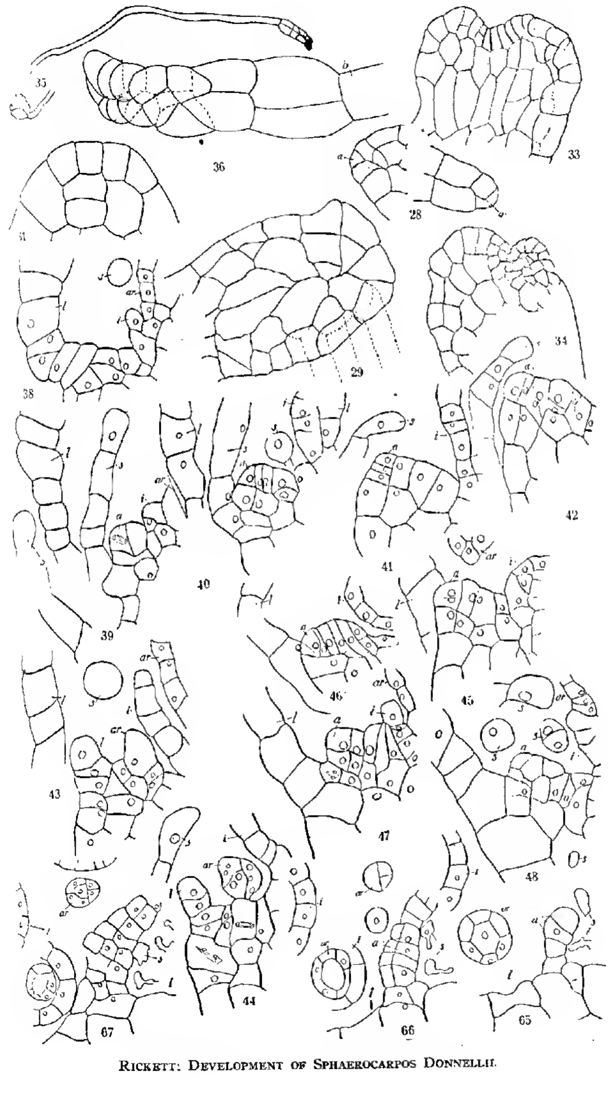
FIGS. 68, 69. Two plants sketched at intervals of a few days in order to follow the origin and growth of the lobes of the thallus. Corresponding letters indicate corresponding lobes in each series. The following table shows the time which intervened between successive sketches.

FIG. 68*A*	March 8.	FIG. 69*A*	March 8.
FIG. 68*B*	" 13.	FIG. 69*B*	" 12.
FIG. 68*C*	" 16.	FIG. 69*C*	" 14.
FIG. 68*D*	" 19.	FIG. 69*D*	" 19.
		FIG. 69*E*	" 22.
		FIG. 69*F*	" 28.

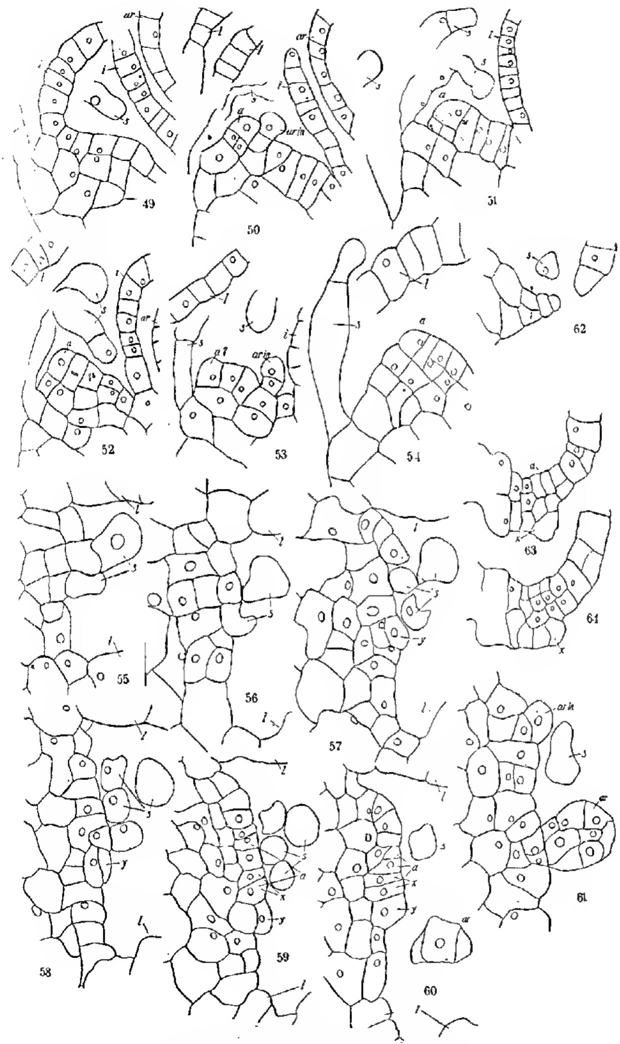
FIG. 70. Plant grown under conditions of excessive moisture in a petri dish



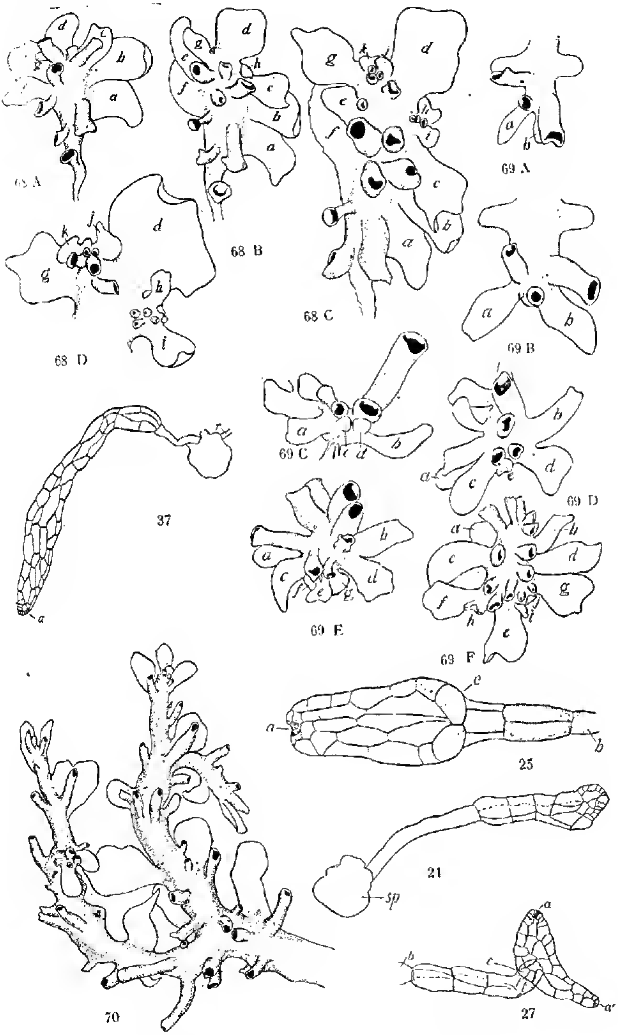
RICKETT: DEVELOPMENT OF SPHAEROCARPOS DONNELLII.



RICKETT: DEVELOPMENT OF SPHAEROCARPOS DONNELLII.



RICKETT: DEVELOPMENT OF SPHAEROCARPOS DONNELLII.



RICKETT: DEVELOPMENT OF SPHAEROCARPOS DONNELLII.

THE GENUS PLANTAGO IN HAWAII

Joseph F. Rock

The Hawaiian Islands possess two endemic species of Plantago, of which one, *Pl. princeps*, is a branching shrub. The only other known species which is a branching shrub is *Plantago fernandezia*, a native of the island of Juan Fernandez. As far as we know *Pl. fernandezia* is not a variable species, while *Pl. princeps* is exceedingly variable and is represented in Hawaii by eight varieties. Curiously enough the typical form has not been collected since the days of Hillebrand.

Plantago princeps is primarily a plant of the lower and drier region, occurring only on the leeward side of Oahu, Kauai, and Molokai. It is true some forms grow near waterfalls (var. *longibracteata*) and exposed to the force of the water, and others grow on drier slopes in stands (var. *elata*). Three varieties of *Pl. princeps* grow usually near water courses (var. *denticulata*, var. *longibracteata*, and perhaps var. *hirtella*). The stemless form (var. *acaulis*) occurs in the rain forest on clay banks, as does var. *Queleniana*. *Plantago princeps* var. *elata* reaches a height of six feet, while var. *denticulata* with a height of four feet is the next tallest; all forms occur from these heights to short, simple stems and stemless plants.

Wawra, who studied the different forms of this and the other species more thoroughly than any previous botanist, lays especial stress, and that rightly, on the venation, which is parallel and free in *Plantago pachyphylla*, while in *Plantago princeps* the lateral veins converge and join the median nerve. The pyxidium dehisces at the base in *Pl. princeps;* in *Pl. pachyphylla* it dehisces at the middle. The seed in *Pl. princeps* is viscous, linear, and black, while in *Pl. pachyphylla* the seeds are supposedly oval, light brown, and not viscous. None of the characters, including the branching and stemless habit of the two species, hold good, nor can they be relied upon as specific characters. This brings us to the conclusion that both species are closely related and even hybridized, which is proven by the numerous forms exhibited by both species. Yet if one should take the very small forms of *Pl. pachyphylla* (var. *pusilla*) from the summit swamp of Kauai, Mt. Waialeale, and compare them with the var. *mauiensis*, one could describe them as distinct species, although there are gradations to be found which to a large extent link these two varieties together.

The main link between *Pl. princeps* and *Pl. pachyphylla* is furnished by a new variety (var. *anomala*) of the former species. That variety has the capsules and leaf venation of *Pl. pachyphylla*, but the seeds and arborescent branching habit of *Pl. princeps*. Variety *acaulis* of this latter species

is also intermediate between the two species and evidently comes closest to *Pl. pachyphylla* var. *hawaiiensis*. It has the capsule and seeds of *Pl. princeps*, but is stemless and has the habit of var. *hawaiiensis* of *Pl. pachyphylla*.

Characters such as pubescence of spike and leaves are not reliable, as glabrous and pubescent spikes occur on one and the same plant. The wool which often covers the under side of the leaves is permanent, while on the spike it is deciduous. Pubescence or slight hairiness disappears often entirely in older plants, while it is present in younger, flowering specimens. The stem in *Plantago princeps* is hairy in var. *Queleniana*, but glabrous between the nodes in other varieties and often even glabrous on the leaf scars. The stamens and style are long exserted in all forms of both species with the exception of var. *Queleniana* according to Gaudichaud's drawing, and also in the typical form as described by Chamisso and Schlechtendal. Male spikes, however, have not been found and that statement cannot be verified at present. As regards the characters of the seeds in the two species, the difference is very slight; the seeds of *Pl. pachyphylla* are not greatly different from those of *Pl. princeps*, and the number of seeds in each locule is also variable. In *Pl. pachyphylla* the seeds are recorded as oval and light brown. The seeds examined of that species by the writer are all dark brown and oblong rather than oval; the margins of the seeds are lighter because of their being transparent.

A decidedly interesting variety of *Pl. pachyphylla* was discovered by the writer on the high, swampy plateau of the Kohala mountains. While the wool in all the varieties of *Pl. pachyphylla* is light brown or fawn-colored, the Kohala variety is densely covered with long, stiff gray hairs. The leaves are very thick and brittle and, including the length of the hairs on both surfaces, are fully 2.5 cm. or an inch thick. The numerous spikes are also densely hairy. This variety grows in sphagnum in open bogs. The capsule and seeds are those of *Pl. pachyphylla;* otherwise the writer would describe it as a new species because of the very different vegetative characters.

One would come to the conclusion that location has a good deal to do with the plant habit; this is not the case with these species, although it may have some influence. The main reason, to the writer's mind, is hybridization, for we find three or four varieties growing together side by side, as is the case with var. *pusilla*, var. *glabrifolia*, var. *rotundifolia*, and var. *kauaiensis* of *Pl. pachyphylla*. So far the first variety has been found only on Kauai, while var. *rotundifolia* occurs also on Maui on the summit swamp of Mt. Eeke, in a modified form (oblong leaves instead of suborbicular). Variety *kauaiensis* is represented by a form (forma *robusta*) both on Maui and Molokai; on the latter island the plant is less robust than on Maui. Variety *glabrifolia* seems to be a large, glabrous form of var. *kauaiensis* and comes very close to large, glabrous forms of forma *robusta* from Molokai. While these intermediates occur, numerous individuals of each apparent variety grow side by side.

Plantago pachyphylla is mainly a bog plant, though the typical form, var. *mauiensis*, grows in the drier regions in the uplands of Haleakala, Maui, along dry stream beds in company with *Geranium tridens*, *Argyroxiphium sandwicense*, *A. virescens*, *Raillardia platyphylla*, *Styphelia Grayana*, etc.

The only other variety, if not a distinct species (var. *hawaiiensis*), grows in the dry cinder on the upper slopes of Mt. Hualalai at 6,000 to 7,000 feet elevation, and also on Mauna Loa, on the island of Hawaii. All the remaining varieties are bog plants or occur immediately below the bogs in moss forests, especially in open places on the ridges. In the bogs they are associated with Viola, *Acaena exigua*, *Geranium humile*, and certain Compositae, as Dubautia and Wilkesia, and on Kauai also with Drosera. Other plants found in its company are *Carex montis eeka*, *Eragrostis variabilis* (on Maui), Scaevola (also on Maui), and Lobelia, as well as Trematolobelia and, on Maui, Argyroxiphium.

Plantago pachyphylla is said to be closely related to *Plantago aucklandica* from the Auckland Islands, while *Pl. princeps* is closely related to *Pl. fernandezia* of Juan Fernandez. The writer has not seen specimens of these two species and is not able to say whether these contentions are correct.

The two Hawaiian species occur on all the islands of the group with the exception of Lanai, Niihau, and Kahoolawe; this does not mean, however, that they never occurred there. In all probability *Pl. pachyphylla* was absent from the two latter islands owing to their dryness and low altitude while it may have occurred on Lanai and there is a possibility that specimens may yet be found there, although that is doubtful, the island being much drier now than it ever was previously.

In working up these difficult and perplexing forms of *Pl. princeps* and *Pl. pachyphylla* the writer had at his disposal the collection in the Gray Herbarium and duplicates of Hillebrand's collection which were given him by the authorities of the Berlin Herbarium.

The writer is indebted to Mr. E. H. Bryan, Jr., a student of the College of Hawaii, for securing references and original descriptions from books not in the College of Hawaii library and for copying the manuscript. He is indebted to Dr. B. L. Robinson of the Gray Herbarium for the loan of the Hawaiian Plantago material in the Gray Herbarium, and he takes this opportunity to express his sincere thanks.

Key to the Hawaiian Species and Varieties of Plantago

A. Lateral veins converging with the median nerve; pyxidium circumscissile at the base (excepting *Pl. princeps* var. *anomala*). — *Plantago princeps.*
- *B.* Stems woody, branching or simple and erect.
  - *C.* Stems simple and erect, not branching.
    - *D.* Stems hairy or woolly their whole length, leaves broadly stem-clasping. — var. *Queleniana.*
    - *D'.* Stems decidedly glabrous, leaves contracted at the base but broader at the insertion. — var. *elata.*
  - *C'.* Stems branching.

D. Leaves petiolate.
E. Leaves glabrous, loosely arranged. — var. *laxifolia.*
E'. Leaves hirtellous or hispid on both surfaces.
F. Petioles slender, distinct. — var. *hirtella.*
F'. Petioles broadly winged, indistinct and broadly dilating at the base. — var. *denticulata.*
D'. Leaves broadly sessile, linear-lanceolate, 30 cm. long by 4 cm. broad, veins parallel; pyxidium dehiscing at the middle. — var. *anomala.*
B'. Plants stemless or very short-stemmed, herbaceous and drooping.
C. Leaves pubescent above with scattered hairs; floral bracts long, acuminate. — var. *longibracteata.*
C'. Leaves glabrous and darker above, pale beneath, with dark-brown pubescence on the prominent nerves below. — var. *acaulis.*
A'. Veins free, parallel or arcuate, not converging; caudex simple, never branching; pyxidium circumscissile at the middle. — *Plantago pachyphylla.*
B. Leaves glabrous on both surfaces or slightly pubescent beneath.
C. Rosettes large; leaves large, 15 to 18 cm. long by 5.5 to 10 cm. broad, glabrous on both sides, 9- to 11-nerved. — var. *glabrifolia.*
C'. Rosettes small; leaves 5 to 6 cm. long, 3- to 5-nerved, often slightly pubescent beneath. — var. *kauaiensis.*
B'. Leaves pubescent, puberulous, or woolly on one or both surfaces.
C. Pubescence or woolliness fawn-colored.
D. Leaves pubescent or woolly beneath.
E. Leaves pubescent beneath, sessile; spike woolly and stout. — var. *mauiensis.*
E'. Leaves orbicular in outline, densely matted below with fawn-colored wool. — var. *rotundifolia.*
D'. Leaves glabrous beneath, strigosely hispid above; plants small, rosette-like; spike few-flowered. — var. *pusilla.*
C'. Pubescence gray.
D. Leaves puberulous, linear-lanceolate; spikes glabrous, slender. — var. *hawaiiensis.*
D'. Leaves thick, brittle, broadly ovate, densely hirsute with gray hairs on both sides; spike hirsute. — var. *muscicola.*

PLANTAGO PRINCEPS Cham. Schlecht. Linnaea 1: 167. 1826.

A shrub 1.3 m. high, branching; branches flexible, terete, naked; leaves deciduous, leaving scars, dilating at the base, semi-amplexicaul, very glabrous, usually 15 cm. long, 2.5 cm. broad, linear-lanceolate, acuminate, narrowed before dilating at the base, 7- to 9-nerved, sometimes oval-lanceolate, shorter, 5 to 7.5 cm. long, 16 to 20 mm. broad, less acute at the apex; margin either entire or denticulate with few minute teeth especially in the upper half; axils woolly, the wool ferrugineous; spike pedunculate, exceeding the leaves, elongate, lax, sparsely flowered, attenuate at the apex; peduncles shorter than the leaves, axillary, compressed, glabrous or with few hairs; flowers lax; bracts glabrous, sometimes ciliate, shorter than the calyx, resembling the sepals but narrower, woolly at the base; calyx 4-sepalous; sepals ovate-acute, the back brown, the margins whitish, mem-

br[illegible]aceous, lightly erose, sometimes ciliate; corolla longer than the calyx, se[illegible]ents erect-spreading, lanceolate, acuminate; stamens inserted at the ba[illegible] of the corolla-tube, *never* exserted; filaments short; anthers oblong, ha[illegible]te at the base, brown; style very long, three to four times the length of [illegible]e corolla; stigma short; capsule scarcely longer than the calyx, ovate-ell[illegible]ical, mucronate, two-seeded in each locule, circumscissile above the ba[illegible]; seeds black.

In the valleys of the lower mountain ranges of Oahu (O-Wahu).

OAHU: Kalihi Valley, Hillebrand in herb. Berlin and College of Hawaii H[illegible]b. no. 16004.

There are no specimens extant in the herbarium at Harvard of the typical *Pl. princeps* Cham. Schlecht. Chamisso states that the stamens are *never* exserted while Hillebrand says "long-exserted." All the varieties referable to this species have long-exserted stamens, with the exception of var. *Queleniana* (Gaud.) Rock which brings that variety closer to the species than any others.

The typical form has not been collected by the writer, nor was it found by Wawra or Heller. Wawra lays especial stress on the venation of the leaves, the veins converging with the median costa below the middle, while those of *Pl. pachyphylla* have the nerves free to the base and parallel to each other.

One exception occurs in *Pl. princeps* var. *anomala*, a new variety collected by Heller on Kauai; the leaves of that variety are those of forms of *Pl. pachyphylla* while the seeds are linear-oblong and black as in *Pl. princeps.* The stem of the new variety is four feet high and branches in a candelabra-like manner, while *Pl. pachyphylla* is stemless. The new variety is apparently intermediate, connecting the two species, or it can be looked upon as a new species; the writer prefers the former interpretation.

Chamisso also says "style glabrous"; the style in the specimen examined is hairy, as in all the varieties of the species. Wawra's statement that the capsules of variety *laxifolia* dehisce at the middle is incorrect.

The only constant character for *Pl. princeps* is the linear-oblong, black seeds. Nervature and branching habit are not constant characters, as stemless plants appear in *Pl. princeps* and the nerves of *Pl. princeps* var. *anomala* are not converging as in all other varieties; the dehiscing of the capsule is also not to be relied upon as a specific distinction, for an exception occurs in the last mentioned variety. From all this it may be seen that *Plantago princeps* is probably the older of the two species.

PLANTAGO PRINCEPS var. **Queleniana** (Gaud.) Rock.

Plantago Queleniana Gaud. Bot. Voy. Uranie 445, t. 50. 1826.

Stem woody, erect, simple, terete; foliose at apex; hairy or woolly all along the stem, especially toward the apex and at the leaf-scars; leaves thick, subcoriaceous, oblong-lanceolate to oval-lanceolate, glabrous on both sides, acute or sub-acuminate at the apex, gradually narrowing at the base,

broadly sessile, partly stem-clasping, 5 to 12 cm. long, 11 to 30 mm. broad, 5- to 11-nerved; nerves converging near the base with the median costa; spikes 1 to 5, more than twice the length of the leaves, peduncles shorter than or equaling the leaves; flowers as in the species; stamens not exserted.

OAHU: Gaud. in herb. Museum Paris; Gaud., Voy. Bonite, in Gray Herb.; U. S. Explor. Exped. in Gray Herb.; J. Remy, no. 427 in Gray Herb. ex herb. Museum Paris; Seemann, no. 2263 in Gray Herb.; Mann & Brigham, no. 85 in Gray Herb.; Manoa Valley, Rock, 1915, College of Hawaii Herb. no. 16001.

Pl. princeps var. *Queleniana* differs from the typical species in the simple, erect stem which is woolly throughout, while that of the species is glabrous. The leaves are not petiolate, but are more or less broadly stem-clasping. The stamens are also included, while in all the other varieties they are exserted. Bennett's *Plantago Queleniana* in the Berlin Herbarium belongs to *Pl. pachyphylla*. Heller's "*Pl. Queleana*," no. 2610, and marked *Pl. princeps* in the Gray Herbarium has nothing in common with this variety; in fact, it represents a very anomalous form.

In Hillebrand's collection in the Gray Herbarium there is a specimen collected in the Kohala mountains from the north coast of Hawaii, which he refers to *Plantago princeps* var. *laxifolia*, but which comes close to var. *Queleniana;* however, owing to the glabrous and somewhat petiolate leaves it is here omitted and referred to var. *laxifolia*.

Pl. princeps var. *Queleniana* is decidedly a montane variety and restricted to the rain forests, while the other varieties including the species occur on the outskirts of the forest and in the drier localities in the lower valleys.

PLANTAGO PRINCEPS var. ELATA Wawra Flora 32: 563. 1874.

Shrub 2 m. high; stem undivided, erect, terete, foliose at the apex, otherwise naked, decidedly glabrous; leaves glabrous, lanceolate, 12.5 cm. long, 2.5 cm. broad, acuminate, narrowing at the base, and about 8 mm. broad at the insertion on the stem, glabrous, shiny above, 9-nerved, the 2 or 4 inner nerves confluent below with the median nerve; spikes many (10 to 20), axillary, twice as long as the leaves; peduncle 7.5 to 10 cm. long, densely flowered, glabrous; bracts half the length of the calyx-lobes; flowers glabrous at the base; calyx lobes ovate-acute; tube of corolla equaling the calyx, the segments linear-lanceolate, acute, reflexed above the calyx; ovary ovate-obtuse; style filiform, long exserted; capsule oblong, twice as long as the calyx, long apiculate, circumscissile near the base, bilocular, locules one-seeded.

OAHU: Mountains of Waianae, Wawra, no. 1728 *b*, in herb. Vienna; specimen not seen.

This is not a synonym of *Queleniana* as cited by Drake del Castillo. It differs from *Queleniana* in the perfectly glabrous stem, which is even glabrous between the leaves. The stem is also unbranched. It is found in the dry regions of the Waianae mountains, while *Queleniana* is a montane species of the rain forest.

This variety differs from the species and from other varieties mainly in the simple, six-foot-tall stem which is glabrous, in the numerous spikes, and in the one-seeded locules. According to Wawra this variety has the appearance of a small palm and forms dense, almost impenetrable stands on the declivities of the lower Kaala range.

PLANTAGO PRINCEPS var. LAXIFOLIA A. Gray, Proc. Amer. Acad. 6: 54. 1866.

Stem 30 to 60 cm. high, more or less woody, hollow, with deciduous wool or straight, silky, fawn-colored hairs in the axils of the leaves; leaves 10 to 15 cm. long, obovate-oblong, submembranous, 4 to 5 cm. broad, acute at the apex, gradually narrowing at the base into a winged petiole of 2.5 to 4 cm., 7- to 9-nerved, glabrous on both sides; spikes numerous, 30 to 45 cm. long, glabrous or with a few hairs at the base of the corolla, densely flowered; corolla-tube one third longer than calyx, segments linear, reflexed; capsules slightly longer than the calyx, obtuse, 4-seeded.

HAWAII: Stones by seaside, north base of Mauna Kea, U. S. Explor. Exped., in Gray Herb., specimen seen.

MAUI: Ravines back of Lahana, Hillebrand ex herb. Berlin, in College of Hawaii Herb. no. 16,002.

KAUAI: Waialeale (about 5,000 feet), no. 2204 in herb. Vienna, Wawra. (Wawra's description agrees well with the type in Gray Herb.)

Variety *laxifolia* which is marked "*laxiflora*" in Gray's handwriting on the type specimen, differs apparently very little from *Pl. princeps* var. *denticulata* Hillebr., the only difference being the hirsute or pubescent leaves and spikes. The denticulation of the leaves in var. *denticulata* is really not a distinguishing character as it occurs in other varieties. Wawra's statement that var. *laxifolia* is the only variety whose stem is glabrous is wrong, as glabrous stems occur also in var. *denticulata*.

Though Wawra's description of his species which he refers to Gray's variety *laxifolia* agrees with the latter's type, with the exception that there are no cilia present in the type on the margins of the sepals, it is hardly believable that plants of such widely differing localities as the beach of the north coast of Hawaii and the summit of Waialeale could be the same. The writer has not seen Wawra's specimens in the Vienna Herbarium and consequently cannot settle the question. There is a possibility that Wawra wrongly recorded the locality. He speaks of having two plants from Waialeale referable to this variety, one a very slender specimen, sparsely flowered and with long petiolate leaves and acute sepals, while the other, a more mature specimen, has a thicker stem, stiffer and shorter petiolate leaves and obtuse sepals. The fact that he says that the latter specimen may come close to a plant described by Gray as *Plantago pachyphylla* var. *hawaiiensis* subvar. *gracilis* leads us to suspect that he actually had a plant of the *pachyphylla* type rather than one belonging to *princeps*, especially as *Plantago pachyphylla* is represented on Waialeale by numerous varieties.

PLANTAGO PRINCEPS var. HIRTELLA A. Gray, Proc. Amer. Acad. 6: 54. 1866.

Stem erect, 60 cm. high, hollow, with permanent wool in the axils or straight, silky hair of a rich brown color; leaves oblong-elliptical, flaccid, 10 to 14 cm. long, 2.5 to 3.5 cm. broad, acute or acuminate at the apex and the base, on slender hirsute petioles of 3 to 5 cm., the latter semi-amplexicaul at the base, hirsute on both surfaces but denser below, 7- to 9-nerved; spikes hirsute, glabrous when old, flexuous, 30 to 45 cm. long; bracts and sepals ciliate, the bracts little more than half the length of the calyx, with a few hairs in the axils.

KAUAI: "Tabular Summit," U. S. Explor. Exped. in Gray Herb.; Waimea (2,000–3,000 feet) Mann & Brigham 613, in Gray Herb.; Waimea (2,000–3,000 feet) Hillebrand, Berlin Herb.

OAHU: Makaleha Valley, Hillebrand, Berlin Herb., specimen not seen.

Variety *hirtella*, while distinct from other varieties, differs only slightly from var. *denticulata* from Molokai and that mainly in the permanent wool on the stem. There is quite a noticeable denticulation present on the leaf of the type specimen as well as on the specimens collected by Mann. The petioles in the present variety are very slender, while in those of Molokai they are broad and stem-clasping.

The distinguishing characters given by Hillebrand as "stem hollow in *hirtella* and solid in *denticulata*" do not hold good, since *denticulata* has also hollow stems or the central cavity is filled with a more or less spongy pith near the base of the stem which makes it appear to be solid.

PLANTAGO PRINCEPS var. DENTICULATA Hillebr. Fl. Haw. Isl. 364. 1888.

Stems 60 to 90 cm. long, with permanent scaly wool in the axils; leaves oblong-obovate, 15 to 25 cm. long, 3 to 5 cm. broad, not distinctly petiolate or the petioles broadly winged, broadly dilating at the base and semi-amplexicaul, hispid on both faces or papillose, 9- to 11-nerved, margins glandular-denticulate; numerous spikes, often 45 to 60 cm. long, hispid when young or glabrous when old, loosely flowered; bracts ciliate, but with very short indistinct hair in the axils; capsules as long as the calyx.

MOLOKAI: Pali of Pelekunu, Hillebrand in Berlin Herb.; Pali of Waikolu, Hillebrand in Berlin Herb., College of Hawaii Herb. no. 16003, and Gray Herb.; Kamoku stream near camp, March 19, 1910, Rock, College of Hawaii Herb. no. 6120.

The stems of this variety are not simple, but branch in a candelabra-like manner; they are not solid as stated by Hillebrand, but hollow as is shown by his own specimens in the Berlin and Gray herbaria. Waikolu plants have more or less glabrous leaves, while those from Pelekunu are hirsute or hispid as are the writer's specimens from Kamoku stream, 1,500 feet lower than Pelekunu.

As has already been stated under variety *hirtella*, the present variety comes close to that variety, but differs in the glabrous stem and broadly

winged or indistinct petioles. The glandular denticulation is the same in both varieties, but is less pronounced in the plants from Waikolu, which specimens are marked var. ***hirtella*** in Hillebrand's own handwriting in the Gray Herbarium.

The plants along the banks of Kamoku stream formed dense clumps or stands several meters in width. In the early spring of 1918 the writer revisited the exact spot, but not a vestige of the plants could be seen.

PLANTAGO PRINCEPS var. **anomala** Rock n. var. (Plate XIII.)

Plantago Queleana Heller in Minn. Bot. Studies 9: 893. 1897.

Plantago princeps Heller ms. in Gray Herb.

Stem 120 cm. high, hollow, dividing at that point into five candelabra-like branches (*teste* Heller), with terminal leaf-clusters; leaves distinctly lanceolate to linear-lanceolate, about 30 cm. long, 3.3 to 4 cm. broad, bluntly acute at the apex, broadly sessile (15 mm. or more broad) at the base (petioles absolutely *wanting*), 11- to 15-nerved; nerves prominent on both sides, absolutely parallel and not converging, glabrous on both sides; spikes 50 cm. long, stout, glabrous; peduncle three-fourths the length of the leaves, densely flowered in the upper half; bracts longer than the calyx, acuminate; calyx segments oval, acute, half as long as the corolla; corolla tube long-exserted, the segments half the length of the part exserted; style glabrous or slightly pubescent; capsule nearly twice the length of the calyx, oblong, dehiscing at the middle; seeds (4) linear, shining, *black*.

KAUAI: Hanapepe valley, ridge opposite Gay and Robinson valley house, July 23, 1895, A. A. Heller, type, no. 2610 in Gray Herb.

This exceedingly interesting variety which Heller refers erroneously to *Plantago Queleniana* Gaud. (*Quelena* Heller), is almost worthy of specific rank. It differs from all other forms of *Pl. princeps* especially in the broadly sessile, very long, lanceolate leaves, with absolutely parallel veins, a character especially laid stress upon by Wawra in distinguishing the two species *princeps* and *pachyphylla*, and in the pyxidium, which is circumscissile at the *middle* and not at the base as in all other forms of *princeps*.

The characters which force us to place this anomalous plant as a form of *Pl. princeps* are the tall, branching stem and linear, oblong, black seeds, characteristic of that species.

Heller's misplacing of this exceedingly interesting plant must have been due to lack of material with which he could compare his specimens, but a careful analysis of the descriptions of the various forms of *Pl. princeps* should have convinced him that he had before him a plant of exceeding interest in so far as it is an intermediate between *Pl. princeps* and *Pl. pachyphylla*.

PLANTAGO PRINCEPS var. LONGIBRACTEATA H. Mann, Proc. Amer. Acad. 7: 189. 1868.

Plantago princeps var. *aquatilis* inclusive of forma *erecta* Wawra, Flora 32: 565-566. 1874.

Plantago Fauriei Lév. Report sp. nov. Fedde **10**: 151. 1911.

Plant herbaceous, drooping, fibrillous; stem very short, about 5 cm., pubescent and with long straight hairs at the leaf scars; leaves narrow-lanceolate, long-acuminate, pubescent above with scattered hairs, more or less abruptly narrowing at the base into a short winged petiole 3 to 3.5 cm. long, broadly subamplexicaul at the base, 7-nerved, the nerves covered with an ochraceous, matted, silky wool, especially in the young leaves; spikes less than twice the length of the leaves; peduncles about 7 to 8 cm. long, glabrous, loosely flowered, the ovate-sublanceolate bracts as long to twice as long as the corolla (11 mm.); sepals acute; flowers with long silky hairs at the base of insertion.

KAUAI: Hanalei, Mann & Brigham, 612, Gray Herb.; Hanalei et Hanapepe Waterfalls, Wawra, 2013*a*, 2013*b*, in herb. Vienna; Hanapepe falls, December, 1909, U. Faurie no. 1078 in herb. Léveillé.

A distinct variety, easily recognized by the long, subovate bracts and long acuminate leaves, whose veins are covered with densely matted, silky wool. It comes undoubtedly close to var. *acaulis*. Its stunted form is probably due to the habitat, as it enjoys the steep rock walls along waterfalls where it is exposed not only to the spray, but also to the force of the water itself.

Wawra records a plant from the same locality, not exposed to the force of water, but as growing in the open places and there developing longer and thicker stems and broader leaves, which he refers to a forma *erecta*. To the writer's mind this procedure is not permissible, because the latter habit of the plant is due to location only.

PLANTAGO PRINCEPS var. ACAULIS Wawra, Flora **32**: 564. 1874.

Root-stock about 15 cm. long, nodose, stem wanting; leaves at the apex of the caudex, densely woolly in the axils or with long, silky hair, oblong-lanceolate, acuminate, 12 to 18 cm. long, 2.5 to 3.5 cm. broad, gradually narrowing at the base into a distinct petiole 3 to 6 cm. long, 7-nerved, pale below, darker above, the nerves prominent below with a dark-brown pubescence, margins entire or minutely denticulate in the upper half; spikes 1 to 4, densely flowered, glabrous, about 25 cm. long including a peduncle of 14 cm.; flowers hispid at the base or glabrous; bracts and calyx puberulous or glabrous; anthers oblong, apiculate, affixed at the middle to the very slender filaments, not exserted; capsule and seed as in the foregoing.

OAHU: on clay location, above Pali, Wawra, no. 1728*a*, in herb. Vienna. Koolau Mts., Punaluu, flowering, Dec. 24, 1908, Rock, no. 391 in the College of Hawaii Herb.; Koolau Mts., Punaluu, flowering and fruiting, June 11, 1916, O. H. Swezey, no. 16,005 in the College of Hawaii Herb.

This variety, while entirely stemless, seems to come close to *Pl. princeps* var. *Queleniana*. It also occurs in the rain forests as does Gaudichaud's *Queleniana*. It is distinguished by the leaves, which are dark above and pale below, and by the prominent nerves, which are somewhat hispid.

PLANTAGO PACHYPHYLLA A. Gray, Proc. Amer. Acad. 6: 54. 1866.

Stemless; rootstock thickly covered with wool; leaves leathery, oval-oblong, ligulate-lanceolate, entire, 5- to 11-nerved, glabrous or tomentulous and puberulous, much shorter than the spike; spike elongate, densely flowered, the flowers woolly at the base (at last often glabrous); bracts and sepals ovate-obtuse or very obtuse; corolla lobes obovate, obtuse or very obtuse, or, after flowering, acute; ovules 2 to 4 in each locule.

PLANTAGO PACHYPHYLLA var. α MAUIENSIS Gray, Proc. Amer. Acad. 6: 54. 1866.

Caudex very thick, densely woolly with long, silky tomentum; leaves broad, 12.5 to 26 cm. long, 3 to 9 cm. broad, ovate, acute at the apex, 9- to 11-nerved, glabrous above, covered with a deciduous wool beneath, veins dark brown, conspicuous below, parallel, arcuate; petioles 2.5 to 15 cm. long, very broad (2.5 cm. or more at the base), the blade gradually narrowing into a short or long, broad petiole; spikes numerous, robust, densely woolly, terete, up to 82 cm. long, 8 mm. in diameter; peduncle as long as or longer than the leaves; rachis shorter than the peduncle; flowers arranged at short intervals in the upper half, woolly at the base: bracts and sepals ovate-obtuse or shortly ovate, with a broad, black median nerve, often pubescent; corolla lobes obtuse or acute; stamens and style long-exserted; ovules in each locule 2 to 4, capsule dehiscing at the middle, obtuse at the apex; seeds oval, dark-brown, almost blackish.

MAUI: U. S. Explor. Exped. on Mauna Haleakala (7,500 feet), type in Gray Herb.; Mann & Brigham, Haleakala, no. 428 Gray Herb.; Wawra, N.E. side Haleakala, no. 1912 Vienna Herb., spec. n.v.; Hillebrand, Haleakala, 6,000–8,000 feet, Berlin Herb., spec. n.v.; Puu Nianiau, slopes of Haleakala (7,000 feet), Rock, September, 1910, no. 8555 in the College of Hawaii Herb. (Under the latter number there are two specimens, one with shorter leaves but not oval, and resembling Mann's no. 428, which must undoubtedly be referred to this variety. The other specimen has much longer leaves with long, very broadly winged petioles, the spikes are very robust, and the sepals and bracts are pubescent while in the typical form these are glabrous.)

PLANTAGO PACHYPHYLLA var. MAUIENSIS forma montis eeka Rock forma nova.

Caudex as in *P. mauiensis;* leaves obovate-oblong or ovate-oblong, gradually narrowing into a very broad, winged petiole, up to 10 cm. long, 2.5 cm. broad at the base; leaves densely matted below with thick, brown wool, with the exception of the clasping base of the petiole, nerves indistinct; spikes shorter than in *P. mauiensis*, robust, densely flowered and covered with matted wool; flowers embedded in the more or less deciduous wool; bracts and sepals oblong, acute or obtuse, as long as or longer than the corolla tube, the broad median nerve densely woolly; corolla lobes short, acute, and glabrous; anthers glabrous, exserted.

WEST MAUI: Slopes of Puu Kukui (6,000 feet), flowering and fruiting, Aug. 21, 1910, Rock, no. 8213 in the College of Hawaii Herb.

(It grew in company with another form with leaves perfectly glabrous beneath, no. 8214.)

This form differs from the typical *mauiensis* in the leaves, which are densely matted with wool beneath instead of being tomentose, and in the nerves, which are consequently indistinct beneath. The median nerve of the calyx is also covered with wool, and the stamens are broader than in the type.

PLANTAGO PACHYPHYLLA var. HAWAIIENSIS A. Gray, Proc. Amer. Acad. 6: 54. 1866. Inclusive of subvariety *gracilis* A. Gray l.c. 55.

Caudex more or less woolly; leaves ovate-lanceolate, broadly lanceolate, linear-ligulate, or lanceolate-oblong, 3- to 9-nerved, narrowed at the base into a very short or slender petiole, 1.5 to 6 cm. long; spike up to 40 cm. long, glabrous or with deciduous pubescence, slender, loosely flowered; sepals nearly all ciliolate, slightly shorter than, or twice the length of, the capsule; capsule oblong to ellipsoidal, 4- to 6-seeded.

HAWAII: Mauna Kea and Mauna Loa (6,000–8,000 feet) "in the environs of the great crater," Remy, 1851–5, no. 429 in Gray Herb.; on lava bed near Kalulu, Mt. Hualalei (6,000 feet), June 10, 1909, Rock, nos. 3722 and 3672 in the College of Hawaii Herb.

Subvariety *gracilis* is not distinct enough to be retained as a subvariety, but must be included in var. *hawaiiensis*. The writer's plants from Hualalei agree very well with Remy's specimen no. 429, but the leaves also agree with Gray's typical *hawaiiensis*. On the same sheet with *hawaiiensis* is a pubescent specimen which Gray marked inter α and β. It is evidently a pubescent form, the pubescence disappearing in older leaves. Hillebrand's specimen belongs to that form. Hillebrand's specimen from Mt. Eeke marked var. *hawaiiensis* does not belong here, but undoubtedly belongs to var. *kauaiensis*, as it agrees fairly well with the type of that variety.

PLANTAGO PACHYPHYLLA var. KAUAIENSIS A. Gray, Proc. Amer. Acad. 6: 55. 1866.

Herbaceous, caudex very short, fibrillous, woolly between the leaves; leaves coriaceous, linear-lanceolate, 5 to 6 cm. long including the very short, broad, sessile petiole, obtuse at the apex, rugose above, 3- to 5-nerved, impressed above, glabrous, pubescent beneath or glabrate; spikes one to several, slender, black, glabrous or hirsute with brownish hairs in the young state, loosely flowered; peduncle slender, 9 to 14 cm. long; rachis of the same length or slightly longer; flowers partly woolly at the base; bracts shorter than the calyx, obtuse; calyx segments obtuse or subacute; corolla segments ovate, acute; anthers broadly ovate, apiculate; style long-exserted, pubescent; capsule exceeding the calyx, dehiscing at the middle, often 1-seeded; seeds oval, pale brown, never viscous.

KAUAI: On tabular summit, U. S. Explor. Exped., type in Gray Herb.; Waialeale, Oct. 20, 1911, Rock, no. 8891 in College of Hawaii Herb. (No.

8891 from the same locality differs from 8891 mainly in the hirsute spike.)

OAHU: Konahuanui, Feb. 22, 1914, O. H. Swezey, no. 12771 College of Hawaii Herb. (Nerves on under side of leaves slightly hairy.)

PLANTAGO PACHYPHYLLA var. KAUAIENSIS forma **robusta** Rock forma nova.

Caudex thick, long, creeping; leaves thick, coriaceous, linear-lanceolate, of nearly even width, broadly sessile at the base, 5 to 17 cm. long, up to 3 cm. broad, 7- to 9-nerved, glabrous on both sides, acute at the apex; spike 22 to 58 cm. long, stout, terete, glabrous or puberulous; bracts and sepals acute, glabrous or puberulous, especially on the median nerve; capsule obtuse, as long as the calyx, 2-seeded.

WEST MAUI: Summit of Mt. Eeke, Hillebrand in Gray Herb. and in College of Hawaii Herb. ex Herb. Berlin; summit of Mt. Eeke, August, 1918, Rock, no. 16006 in College of Hawaii Herb.

(The W. Maui plants referred by Hillebrand to *hawaiiensis* cannot be separated from var. *kauaiensis*, but differ in the much stouter, terete spikes. The writer's specimens from Mt. Eeke have slender spikes as in the typical *kauaiensis*, but are pubescent and glabrous afterwards and, in some instances, floriferous almost to the base.)

MOLOKAI: Kawela Swamp below Pelekunu, growing with Oreubulus and Panicum, March 17, 1910, Rock, no. 6098 in College of Hawaii Herb.

(Although the Molokai plant is less robust than the Maui form it cannot well be separated from it. The leaves are slightly pubescent on both surfaces and more flaccid. The leaves are glandular-denticulate and somewhat pubescent, especially on the nerves.)

The hairiness of the spike is evidently an unreliable character, as hairy and glabrous spikes occur on identical plants.

The writer's specimen (no. 8214) from Puu Kukui, West Maui, are identical with those of Hillebrand from Eeke. It is exceedingly doubtful if Hillebrand had ever visited Mt. Eeke, which doubt seems to be confirmed by the fact that he makes no mention of the thousands of silverswords occurring there and which are practically absent from Puu Kukui.

PLANTAGO PACHYPHYLLA var. KAUAIENSIS forma **intermedia** Rock forma nova.

A specimen collected on Waialeale, Kauai, no. 8891*a*, with hirsute spikes and leaves hirsute on the upper surface, is intermediate between *kauaiensis* and Wawra's variety *pusilla*.

Plant larger, leaves linear-oblong, glabrous and prominently nerved below, strigosely hispid above, but finally deciduous with the exception of the apices of the leaves; spikes shorter, covered with deciduous hairs, rachis longer, angular; calyx segments acute, otherwise as in var. *pusilla*.

KAUAI: Waialeale, Oct. 20, 1911, Rock, no. 8891*a* in College of Hawaii Herb.

Forma *intermedia* differs from the typical *pusilla* in being a larger plant, in the more robust spikes, which are many-flowered and hirsute, and in the acute sepals. It differs from *kauaiensis* mainly in the linear-oblong leaves, which are strigosely hispid toward the apices, and in the shorter spikes. It forms the transition type between varieties *kauaiensis* and *pusilla*.

PLANTAGO PACHYPHYLLA var. PUSILLA Wawra, Flora 33: 568. 1874.

Herbaceous, rosette-like; caudex very short, woolly between the leaves; leaves numerous, coriaceous, 2 to 4 cm. long, 4 to 6 mm. broad, oblong, spathulate, acute or rounded, 3- to 5-nerved; blades glabrous below, strigosely hirsute above with yellow articulate hairs, entire; spikes (1 to 7) 4 to 15 cm. long; peduncle glabrous, shining, slender, floriferous on its upper third or fourth and bearing from 3 to 5 flowers; rachis glabrous, but flowers woolly at the base; bracts half the length of the calyx, glabrous, rounded; sepals rounded, glabrous; corolla lobes linear-oblong, membranous, obtuse, one fourth the length of the tube; capsule shortly acute, dehiscing at the middle, 4-seeded; seeds reddish-black, oblong or ovoid-oblong, minutely wrinkled.

KAUAI: Plateau of Waialeale, no. 2166 Wawra, in Herb. Vienna, spec. n.v.; Waialeale, Oct. 20, 1911, Rock, no. 8890 in College of Hawaii Herb.; Waialeale, Oct. 20, 1916, Rock, no. 16007 in College of Hawaii Herb.

No. 16007 seems to be the typical *pusilla*, while no. 8890 is somewhat larger, the leaves being woolly below, at least along the nerves.

PLANTAGO PACHYPHYLLA var. ROTUNDIFOLIA Wawra, Flora 32: 567. 1874.

Caudex very short, fibrillous; leaves rosette-like, coriaceous, obovate or almost orbicular, 5 to 7.5 cm. long, narrowing at the base but not really petiolate, glabrous above, covered with a thick ochraceous stuppeus indumentum, 5-nerved; nerves arched, impressed above, invisible below; spikes one or two, erect, covered with a silky pubescence, rachis shorter than the peduncle, densely flowered; flowers woolly at the base, at length naked; bracts obtuse; calyx segments obtuse; corolla lobes broadly ovate, obtuse; capsule equaling the calyx, circumscissile at the middle, bilocular, 2-seeded; seeds broadly ovate, yellowish brown, never glutinous.

KAUAI: Waialeale, high plateau in moss on trunks of trees, Wawra, no. 2201 in herb. Vienna, spec. n.v.

PLANTAGO PACHYPHYLLA var. ROTUNDIFOLIA forma **crassicaudex** Rock forma nova.

Caudex very thick, 10 cm. or more long; leaves obovate-oblong, with revolute margins, densely woolly below as in the variety, glabrous above; otherwise as in variety *rotundifolia*.

MAUI: Mt. Eeke, August, 1918, Rock, no. 16008 in College of Hawaii Herb.

The writer establishes this form rather reluctantly as there are no mature spikes present on the single specimen collected, and only dead

spikes remain. It differs, however, sufficiently from variety *rotundifolia*, especially in the thick 10-cm. long caudex and in the obovate-oblong leaves.

PLANTAGO PACHYPHYLLA var. GLABRIFOLIA Rock, Indig. Trees Haw. Isl. : . 1913.

Caudex very short, thick, and matted with wool; leaves forming large rosettes, broadly ovate in outline or ovate-oblong, acute, thick coriaceous, glabrous on both surfaces, broadly sessile at the base, 9- to 11-nerved, the nerves prominent below, the lateral ones arcuate, margins inconspicuously glandular-denticulate, 15 to 18 cm. long, 5.5 to 10 cm. broad; spikes 1 to 4, stout, glabrous or pubescent in the young stage, densely flowered in the upper third, flowers crowded toward the apex, loosely flowered toward the base of the rachis; bracts as long as the calyx, obtuse; sepals acute; corolla lobes acute or obtuse, reflexed; style long-exserted, gray-hairy; anthers more or less excised at the base, oblong to ovate; capsules unknown.

KAUAI: Waialeale, Oct. 20, 1911, Rock, no. 8889 in College of Hawaii Herb.

This variety differs from the others in the very broad, almost orbicular leaves which are glabrous on both surfaces, and in the glabrous spikes which are densely flowered, the flowers being oblong in outline rather than oval. With the exception of its glabrousness it would be referable to the typical *Plantago pachyphylla* var. *mauiensis*.

Variety *kauaiensis* and its forma *robusta* from Maui and Molokai undoubtedly are very closely related and are perhaps only forms of *Pl. pachyphylla* var. *mauiensis*, although large-leaved glabrous forms grow together with hirsute, slender and robust forms in the same locality.

PLANTAGO PACHYPHYLLA var. **muscicola** Rock. var. nova.

Caudex short, thick, densely fibrillous below, the roots densely hairy as is the whole plant; leaves ovate to ovate-oblong, brittle, thick, fleshy, about 2 cm. or more in thickness, including the dense, gray hairs on both surfaces, these sometimes at right angles to the blade, 15 to 20 cm. long, 5 to 8 cm. wide, acute at the apex, contracted below but broadly sessile at the base, 7- to 9-nerved; nerves inconspicuous owing to the pubescence, arcuate; margins of the leaves more or less conspicuously glandular-denticulate; spikes numerous (up to 10), densely hairy, stout, terete; bracts as long as the calyx or longer, hairy; sepals broadly ovate, acute, ciliate at the apex; corolla lobes broadly oval, acute, 1-nerved; capsule exserted, oblong, obtuse, 2-seeded; seeds oval, dull brownish, rounded at both ends.

HAWAII: Below summit of Kohala Mts. back of Waimea, elevation 4,200 feet, in open bog, embedded in thick sphagnum, June, 1910, Rock, no. 8315 in the College of Hawaii Herb.

This interesting variety differs from all the others in the thick, brittle, fleshy leaves which are densely hirsute on both surfaces with long, gray hairs which stand at right angles to the blade. The numerous spikes are very robust and hirsute as are the leaves. Otherwise as in *Plantago pachyphylla*. Specimens of this variety have been distributed to herbaria as *Plantago muscicola*.

Introduced Species

Plantago major L. Sp. Pl. 1: 112. 1753.

Hawaii: Makahalau, Parker Ranch, June 25, 1909, Rock, no. 3 46 in College of Hawaii Herb.

Oahu: Pauoa Valley, Oct. 24, 1908, Rock, in College of Hawaii Herb.

This species is now distributed over all the islands along roadsides and pastures. It is a native of Europe and Asia. On Hawaii the largest specimens have been collected. It is of early introduction.

Plantago lanceolata L. Sp. Pl. 1: 113. 1753.

Hawaii: Waikii, 5,000 feet elevation, July, 1909, Rock, in the College of Hawaii Herb.

Kauai: Hanapepe river basin, June 28, 1895, Heller, no. 2457 in the College of Hawaii Herb.; Kaholuamano, July, 1909, Rock, no. 5728 in the College of Hawaii Herb.

This species, also a native of Europe, made its appearance in the Hawaiian Islands only within the last 25 years or so. It was first observed on the island of Kauai. It was introduced with impure grass or flower seed by Gay and Robinson from Australia, where the plant has been proclaimed. It is abundant at Kaholuamano (elevation 3,400 feet), where it even crowds out grasses.

Plantago virginica L. Sp. Pl. 1: 113. 1753.

Hawaii: Parker ranch, June 24, 1909, Rock, nos. 3138 and 3139 in the College of Hawaii Herb.

This species is a native of North America, where it occurs from Rhode Island to Florida and has also been collected in the Bermudas. On Hawaii it is very common on the pasture lands of the Parker ranch, especially at Kanahiokaoka in Mana, and Paauhau, at an elevation of about 3000 feet. Some of the paddocks are completely taken possession of by this species, the rosettes of which are flat on the ground and not erect.

Doubtful Species

Plantago Gaudichaudiana Lév. Rept. Sp. nov. Fedde 10: 151. 1911.

"Pulcherrima species his notis facile diagnoscenda; stirpe foliorum emortuorum vaginis foliis laceratis obtecta; scarpa striato glabro circa 70 cm. alto, virgato, erecto; folia radicalia glabra 5 nervia, 20 cm. circiter longa et 1 cm. lata nec dilatata; spica 30 cm. alta; flores numerosi, dissiti, sparsi, subverticillati; bracteis concavis, brunneis, acuminatis; sepala nigro-brunnea margine scariosa obtusata style brunneo exserto.

"Haec est, mea sententia, illa planta, cui speciminibus maximis visis, Gaudichaud nomen nudum *quelea* imposuit."[1]

Hawaii: Mauna Kea, 2,000 meters, June, 1909 (Faurie, no. 1075).

[1] In the writer's opinion the plant is referable to one of the many forms of *Plantago pachyphylla*, probably to var. *hawaiiensis* Gray.

ROCK: PLANTAGO PRINCEPS VAR. ANOMALA ROCK. PHOTOGRAPH OF TYPE IN THE GRAY HERBARIUM.

RELATION OF CATALASE, OXIDASE, AND H^+ CONCENTRATION TO THE FORMATION OF OVERGROWTHS

R. B. Harvey

Overgrowths were found by the author (7) to result from local freezing of the leaf tissue in a number of plants, including cabbage (*Brassica oleracea capitata*) and *Bryophyllum calycinum*. These overgrowths offer special opportunity for the separation of certain factors concerned in the rejuvenescence of cells, and for the comparison of physiological conditions attendant upon the production of overgrowths resulting from infection with *Bacterium tumefaciens* and from the stimulation of normal tissue by physical and chemical means. The literature of overgrowths as a result of bacterial infections in plants has been fully presented in papers by Dr. Erwin F. Smith.

The economic importance (9, 19, 20) of certain plant diseases in which overgrowths are produced, and the relation of these to growths of similar nature occurring in man and other animals (3, 4, 5), have had sufficient discussion in recent articles (6) to make comment unnecessary in this paper. The production of intumescences by means in which bacteria are not concerned has been noted recently by Smith (2) and Wolff (1).

In a paper by Dr. Erwin F. Smith (2, p. 167) it was suggested that osmotic relations between tumor and healthy tissues might offer an explanation for overgrowths. With a view to determining these osmotic relations the author has determined the freezing points of tumor and healthy tissues in different plants. It now appears that determinations referred to in a publication by Dr. Smith (3, p. 441) may be in error on account of the difficulty in obtaining the true freezing point of the tissues from the freezing point of the expressed juice.

The freezing point of tumor and healthy tissues taken from the same plants was obtained by expressing the juice with a Buchner hand press, and with an hydraulic press using 10 tons on a 2½ inch ram.

The freezing point of juices expressed from a tissue vary according to the treatment before expression and also according to the pressure applied (7, p. 94). Also, it appears that variation in the quantity of wood in the tissue prevents one from obtaining a uniform sample by pressure.

In table 1 are given the freezing points of juices expressed after freezing with solid CO_2 and grinding in a mortar while frozen dry. Stem tissue was taken from nodes immediately adjacent to the tumors. The tumor material was supplied by Dr. Smith's laboratory and was produced by inoculation with *Bacterium tumefaciens*.

TABLE 1. *Freezing points of juices from tumor and healthy tissues*

	Ricinus	
Leaf	− 0.793° C.	− 0.815° C.
Tumor	− 0.953 C.	− 0.746 C.
Stem	− 0.712 C.	− 0.590 C.
	Daisy	
Leaf	− 0.810° C.	
Tumor	− 1.170 C.	
Stem	− 0.783 C.	
	Beet	
Leaf	− 0.920° C.	
Tumor	− 0.970 C.	
Root	− 1.210 C.	

In Ricinus and daisy the tumor tissue yields an expressed juice with a greater freezing-point depression than that of adjacent normal tissue. But there is more woody tissue in the normal stem than in the tumor tissue of the Ricinus and daisy. The author does not regard these freezing points as the true values for the tissue. They are given for the purpose of showing the errors which may arise from the method of obtaining the freezing points of these tissues.

By using a thermocouple threaded through the tissue the freezing point can be obtained directly. The apparatus used in these determinations was the same as that reported in a previous paper (18). A piece of tissue of the same size in each case was threaded upon the thermal junction and cooled by ether evaporation to a desired point. Inoculation of the tissue was brought about by knocking it against the wall of the surrounding tube which was covered with frost. By this means the undercooling could be regulated quite accurately. When the undercooling is the same, the freezing points of the tumor tissue and of adjacent healthy tissue are nearly the same; in any case there is only a few hundredths of a degree difference, as shown in table 2.

TABLE 2. *Freezing points of tumor and healthy tissues obtained by thermocouple*

	Undercooling	Freezing point
	Ricinus	
Tumor	− 1.49° C.	− 0.40° C.
Healthy stem	− 1.49 C.	− 0.41 C.
Tumor	− 2.20 C.	− 0.60 C.
Healthy stem	− 2.37 C.	− 0.64 C.
	Beet	
Tumor	− 2.92° C.	− 1.38° C.
Healthy root	− 2.90 C.	− 1.33 C.
Tumor	− 4.44 C.	− 1.74 C.
Healthy root	− 4.46 C.	− 1.72 C.

These values are free from errors arising in expression of the juice and represent the true freezing points of the tissue. They are of greater value than those made on expressed sap because small pieces of tissue can be taken immediately adjacent. Since such good checks were obtained, the author is inclined to believe that there is but little difference in the osmotic concentration in these particular cases.

Juices expressed from tumors produced by inoculation with *Bacterium tumefaciens* show a hydrogen-ion concentration consistently a little lower than that of juices expressed from healthy stem tissues taken from adjacent nodes, as shown in table 3.

TABLE 3. *H^+ concentrations of tumor and healthy tissues*

	Ricinus P_H	$C_H \times 10^6$
Tumor juice	5.822	1.51
Healthy stem juice	5.411	3.88
Leaf juice	5.580	2.63
Tumor juice	5.886	1.30
Healthy stem juice	5.817	1.52
Leaf juice	5.739	1.82
Tumor juice	5.62	2.40
Healthy stem juice	5.35	4.47
Leaf juice	5.48	3.30
	Beet	
Tumor juice	6.347	0.42
Healthy root juice	5.818	1.52

These tumors were in actively growing condition. The juice was expressed after grinding in a meat chopper but without freezing the tissue, since the hydrogen-ion concentration of a juice has been shown to be changed by the precipitation of the proteins on freezing the tissue. The determinations were made by the potentiometric method.

It may be suspected that the expressed juice will show a H^+ concentration different from that of the cell sap of the vacuoles owing to errors arising by expression. This may be the case in some tissues. However, the author has been able to dilute the juice from such tissues as tomato fruit to one fifth the original concentration without appreciably changing the H^+ concentration. The H^+ concentration within the uninjured cells can be estimated only in tissues which have natural indicators.

The concentration of the buffer salts present in the tissue will determine whether or not they are able to maintain the original P_H value on dilution. Precipitation of globulins on too great dilution of the juice may bring about H^+ changes. The H^+ concentration of a buffer solution depends (within fairly wide limits) upon the ratio of the buffer substances present, and not upon their total concentration. In obtaining the freezing-point depression,

the total concentration of the expressed juice must be the same as that within the tissue to obtain a true value; for the H^+ concentration this is not necessarily the case.

Although the differences in H^+ concentration shown in the above table are small, they may be of relatively great importance for the activity of the respiratory enzymes associated with growth. The curve for the activity of catalase of plant origin at various H^+ concentrations is practically the same as that for catalase of animal origin given by Michaelis (8). From this curve it will be seen that the H^+ concentration shown by the plant tissue lies in a critical region for the activity of catalase. A change from P_H 5.52, the average value for healthy stem tissue of Ricinus, to P_H 5.78, the average value for tumor tissue, increases the catalase activity 25 percent at an acetate concentration of fiftieth normal. The activity of oxidase is increased also by a decrease in the H^+ concentration. In a paper cited above (7, pp. 98–101) the author gave indications of the decrease in H^+ concentration resulting from freezing of leaf tissue. Areas of Bryophyllum leaves which contain anthocyanin are changed from red to blue on freezing. This is not necessarily accompanied by death of the tissue.

It is shown from the work by Dr. Smith and others (9, p. 113) that *Bacterium tumefaciens* blues litmus milk and decreases the H^+ concentration of the culture medium. This it appears to do also in the tissue in which it grows.

Since catalase is destroyed at increasing rates with increase in the hydrogen-ion concentration, it is of interest to compare the catalase activity of two tissues of the same plant which were the same before overgrowth was induced by stimulation but which finally have different hydrogen-ion concentrations. For this purpose, Ricinus plants were inoculated with *B. tumefaciens* and when the tumors had become sufficiently large they were removed. Healthy stem tissue was taken from the same node. Fifty grams of tissue were ground in a mortar with crushed quartz and 25 cc. of phosphate buffer mixture C_H 2.7×10^{-8}, and made up to 500 cc. with distilled water. The Van Slyke apparatus for amino-acid determination was found convenient for catalase determination when used in a constant temperature room. Five cc. of hydrogen peroxide (Oakland 3 percent neutral) was run into the reaction chamber of the apparatus and washed down with 10 cc. of distilled water. After adjusting the level in the measuring pipette, 10 cc. of plant tissue dilution was run in from the side burette. The apparatus was shaken only fast enough to give a good mixing of the solution, and the rate of shaking was kept the same throughout. After 10 minutes the following amounts of oxygen were evolved at 30° C.

Tumor tissue	44.6 cc. O_2	42.3 cc. O_2
Healthy stem tissue	13.2 cc. O_2	13.3 cc. O_2

Bryophyllum leaves were inoculated with *B. tumefaciens* by injecting a

suspension of the bacteria into the leaves by means of vacuum. This produced rather large tumored areas. Healthy leaf tissue which showed no tumor formation was taken from the same leaf. Three and three tenths grams of tumor and healthy tissue were diluted to 50 cc. after treating as before. Twenty-five cc. of these dilutions gave in the same time for tumor tissue 38.9 cc. O_2; and for healthy leaf, 2.4 cc. of oxygen.

Intumescences were also induced on Bryophyllum leaves by freezing the plants at a temperature of $-2°$ C. After about 15 minutes it was observed that frozen areas appeared over the surface of the leaf. The plants were removed from the cold chamber when the areas were about 5 mm. in diameter and placed in the greenhouse. After five days the areas had grown into small intumescences. While these were still actively growing, leaves were selected in which the tumors formed about half the area. It was found impossible to get a greater percentage of the area to grow out as intumescences because death occurred if more than about half the leaf surface was frozen. The tumor spots were so small and so intermingled with healthy tissue that a quantitative separation of the tumored and healthy areas could not be made without introducing great error.

Six grams of leaf tissue of which the tumored areas were estimated to represent half the tissue were taken and compared for catalase activity with 6 grams of normal tissue from a leaf of the same age and size from the same plant. The tissues were ground with quartz and excess $CaCO_3$ and made up to 200 cc. Twenty-five cc. of the dilution were taken with 5 cc. of the hydrogen peroxide. After 15 minutes the following amounts of oxygen were evolved:

Tumor 50 percent	3.1 cc. O_2
Healthy tissue	1.05 cc. O_2

Tissues of beet in which the overgrowths were produced by inoculation with *B. tumefaciens* gave on treatment in the exact manner given above for Ricinus tissue:

Tumor tissue	8.1 cc. O_2	8.9 cc. O_2
Healthy root tissue	5.6 cc. O_2	5.4 cc. O_2

It should be noted that the increase in catalase activity of the intumescences produced no Bryophyllum leaves by *Bacterium tumefaciens* is much greater than that of the intumescences produced by freezing.

The peroxidase and catalase activities in intumescences of cabbages induced by freezing are greater than those in normal tissues of the same leaf.

Since this decrease in H^+ concentration increases the catalase activity, it is interesting to note that the catalase activity is greatly decreased in mosaic leaves of tobacco which show greater H^+ concentration than healthy leaves. In this case also, the P_H values are but slightly different, yet it appears of great physiological importance for the growth of the mosaic-diseased cells.

The oxidase activity of tumor and healthy tissue was obtained on beets

inoculated with *B. tumefaciens*. Tissue dilutions representing the same green weight of material were made up to C_H 3.6 $\times$ 10^{-7} and $n/60$ total salt concentration. Oxidase determinations were made in an oxidase apparatus which has been described in another place (10) and which is a modification of the simplified Bunzell (11) oxidase apparatus (12). After shaking for four hours at a constant temperature of 30.2° C., the following readings were given as the average of three determinations:

Oxidase activity of beet tissue

Tumor tissue	
Hydrochinone	3.24 cm. Hg.
Pyrogallol	4.14 cm. Hg.
Healthy tissue	
Hydrochinone	0.90 cm. Hg.
Pyrogallol	1.70 cm. Hg.

In this case it appears that the oxidase activity in the tumored areas is greatly increased. An increase in oxidase activity in tumored tissues has been reported in a number of articles (22).

In this connection it is interesting to note that the anthocyanin color is greatly increased in the tumored areas of Bryophyllum leaves induced by freezing, so that the intumescences stand out as red areas. The intumescences are produced mostly along the veinlets rather than in the vein islets. The deepest color of anthocyanin is located along the veinlets within the intumescences.

When Bryophyllum leaves are frozen in spots over a small percentage of the area, the frozen spots turn brown. One can predict from the depth of this brown color whether the area will die or will be stimulated to growth. As the percentage of the total area which is frozen increases, the depth of brown color in the spots decreases. When the whole leaf is frozen the color is uniformly distributed. If brown-spotted leaves are killed by freezing or by ether, the spotted areas maintain the deepest color, showing that the oxidizable substances have been partly removed from the surrounding tissues. It appears from this that there is an accumulation of the colored compounds within the frozen areas. This becomes very marked about 12 hours after freezing, as shown in the photograph (fig. 1). The greatest development of color occurs along the veinlets within the frozen areas (fig. 2). The frozen areas seem to have the property of taking up substances from the surrounding tissues which are converted within them and which accumulate as brownish colored compounds. Onslow (13) has given us data on the nature of such substances. Substances of the type of catechol occur in plants which brown on injury. Peroxidase activates the oxidation of these aromatic compounds, and the oxidized product is an organic peroxide.

It has been shown by Krassnosselsky (14) that an increased rate of respiration follows frost injury. The author so far has not been able to

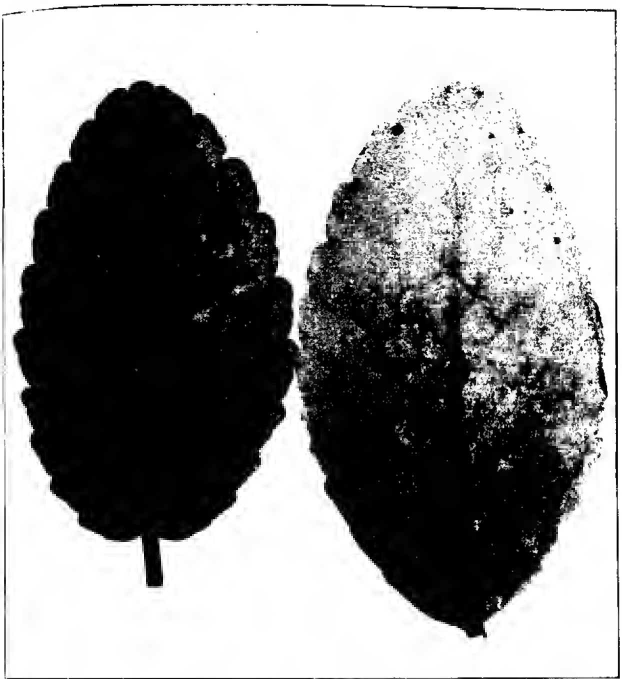


FIG. 1. Development of color in Bryophyllum leaves as a result of freezing. Notice the deep color in the small isolated frozen areas and the decrease of the color intensity with increasing size and frequency of the spots. The leaf with uniform color distribution was frozen throughout.

compare the respiratory rate of the frozen and normal areas. It would be desirable also to determine the oxygen acceptors in these spots. There is no immediate increase in the catalase activity of the areas frozen, nor does this increase until growth can be observed. Blackening indicates that there is an abnormally oxidized condition in the frozen areas.

DISCUSSION

To the author it seems plausible that the hydrogen-ion concentration of the cell sap in the frozen areas may be decreased by removal of H^+ during

the precipitation of proteins, which has been shown by the author to occur on freezing (7, p. 103). This decrease of H^+ concentration favors the activity of catalase and oxidase. The author has shown (7) that in hardened cabbage leaves there is no production of intumescences from frozen plants. The reason ascribed for this was that there was no permanent combination of protein and H^+ and hence no H^+ change or protein precipitation in this case. There may be attendant upon the protein precipitation, which could occur especially at the outer boundary of the protoplast, an increased

FIG. 2. Intumescences on Bryophyllum leaf induced by freezing. Notice occurrence of intumescences along the veinlets and the brown color along the veins in the light-colored areas. Light-colored areas are due to death of tissue because too great a percentage of the area was frozen. Local freezing occurred in these areas along the veins only, and brown color developed there. Subsequently the cells in the light-colored areas died. Renewed growth is not due to isolation, for three islets of normal tissue occur in the upper portion of the leaf and these show no renewed growth.

permeability of the membranes for oxygen, so that the oxygen concentration within the cell is increased. The next attendant condition would be the formation of increased quantities of organic peroxide. The oxidation proceeds to the formation of colored compounds, finally producing substances such as purpurogallin from pyrogallol or melanins from tyrosine. The oxydo-reductases are prevented from normally reducing these colored compounds by the increased concentration of oxygen in the cells (15).

If the cell has been injured to such an extent as to be killed, all the oxygen acceptors are changed to the final state of equilibrium with the air. In case the cell recovers, an increased rate of oxidation has been established in it above the rate of oxidation in the cells in areas not frozen, owing to the greater concentration of organic peroxide and decreased H^+ concentration.

Child (16) has shown that dominance of growth is conditioned by a higher rate of metabolism in the growing region than in the surrounding area. When this increased rate is once established, it then opens the way for further growth at the expense of the surrounding tissue. In case too great a percentage of the leaf cells are frozen, there is no great concentration and transformation of the oxygen acceptors in any one area, as shown by little development of brown color. Hence there is little growth produced, because no one frozen area dominates a sufficiently large area of normal tissue which supplies it. This is actually the case. The most rapidly growing areas are small and somewhat scattered. Loeb (17) has suggested that the quantity of growth in *Bryophyllum calycinum* is conditioned by the quantity of some growth-promoting substances within the leaf. It is entirely possible that the usual sources of energy, the carbohydrates, are not the only substances concerned, but also that there are chromogenic substances of equal importance. Oxidase determinations indicate that there may be such substances produced or accumulated in plant tumors caused by *Bacterium tumefaciens*.

Loeb (21) also suggests that the dominance of a growing apex is due to the production within it of inhibiting substances which hold in check the neighboring buds. The difficulty with this assumption is that if the inhibiting substance is produced in the dominant apex it should depress growth there also since it would be in greatest concentration there. This ought to be a general objection to such assumptions. It seems to the author more plausible to assume that in correlation of growth the dominance of a growing area is conditioned not by the production of an inhibitor for the area around it, but by the removal from the surrounding area of growth-stimulating substances and their accumulation in the dominant area. These growth-stimulating substances, such as the chromogens of Palladin (23), are produced by all the cells and are diffusible. We have seen in a case cited above (*Bryophyllum*) how they accumulate in a frozen area and are associated with a renewal of cell growth.

In the case of inoculation of tissues with *Bacterium tumefaciens*, the presence of this bacterium favors the action of the respiratory enzymes by locally decreasing the H^+ concentration. This condition is continuous, and hence the growth process should be continuous. The bacteria in such tumor tissue evidently do not produce substances detrimental to cell multiplication, but may produce substances which favor oxidation within the tissue.

Summary

It was found that the concentration of osmotic substances was the same in tumor and healthy tissues in Ricinus and beet when measured by the thermocouple method. Hence osmotic relations do not account for the tumor production by *Bacterium tumefaciens* in these cases.

Catalase, oxidase, and peroxidase activity is greater in tumor tissue than in adjacent healthy tissue either when the tumors are produced by inoculation with *B. tumefaciens* or by freezing.

Growth in frozen spots of Bryophyllum leaves is correlated with the accumulation within them from the surrounding tissue of substances of the nature of catechol, which are transformed by oxidation into colored compounds.

The H^+ concentration of tumors produced both by freezing and by bacterial inoculation is consistently less than that of adjacent healthy tissue.

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